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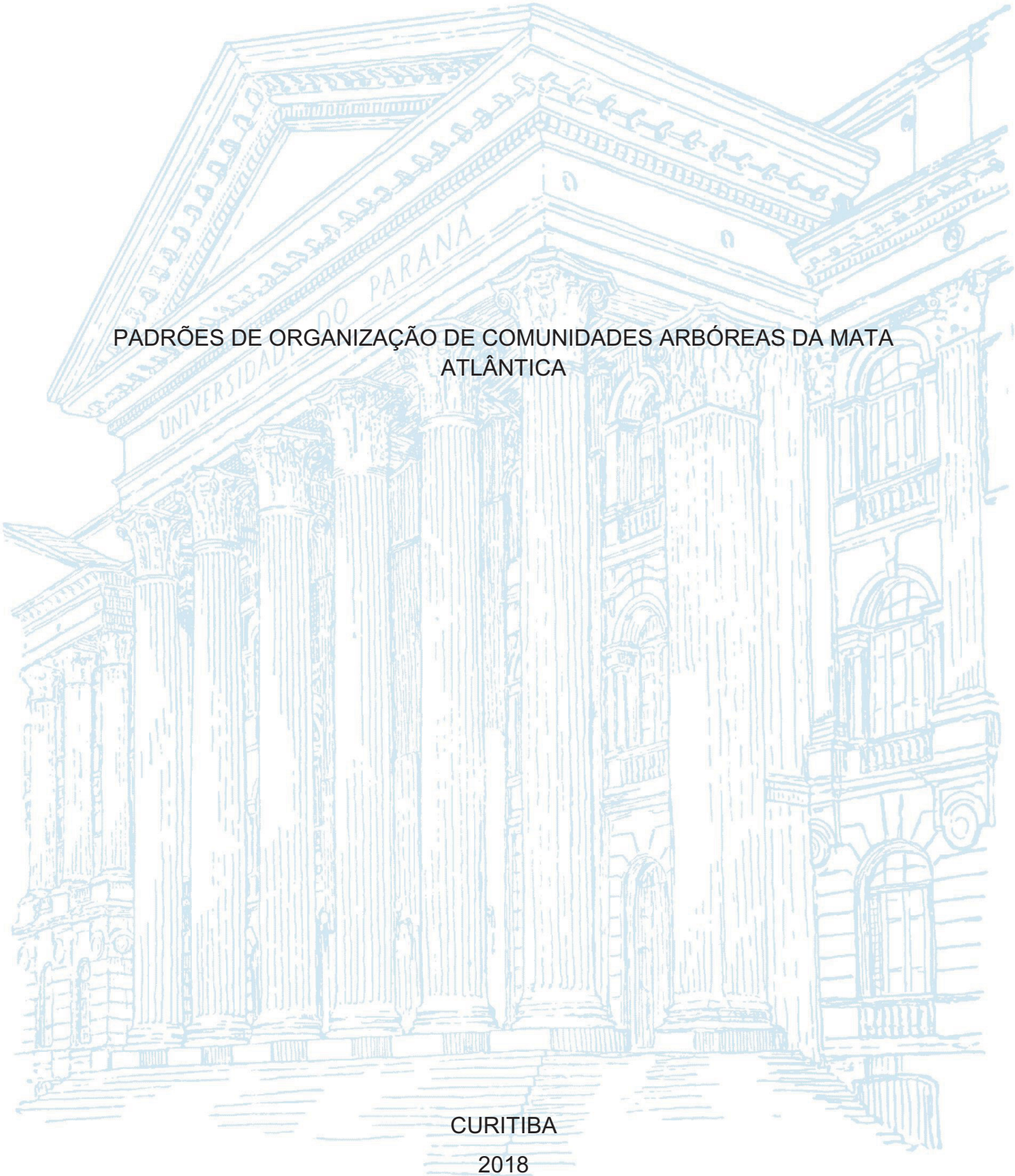
DANIELE APARECIDA DE MORAES




# PADRÕES DE ORGANIZAÇÃO DE COMUNIDADES ARBÓREAS DA MATA ATLÂNTICA

CURITIBA

2018

DANIELE APARECIDA DE MORAES

# PADRÕES DE ORGANIZAÇÃO DE COMUNIDADES ARBÓREAS DA MATA ATLÂNTICA

Tese apresentada ao curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutora em Ecologia e Conservação.

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Curitiba, 13 de Julho de 2016.

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*Dedico esta tese à memória de minha querida mãe, Azenir de Moraes (1953 -2016).*

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## RESUMO

Um dos maiores desafios da ecologia é desvendar os processos responsáveis por gerar padrões de diversidade em diferentes escalas. Esse desafio se torna especialmente intrigante em regiões altamente biodiversas, como as florestas da Mata Atlântica brasileira. Em escalas locais, espera-se que os processos relacionados ao nicho das espécies (filtragem ambiental e interações bióticas) expliquem grande parte dos padrões de composição e riqueza de espécies. Assim, o emprego de diferentes abordagens que capturam aspectos distintos do nicho se torna fundamental para elucidar esses processos. Para esta tese, nós realizamos uma amostragem intensiva de espécies e atributos funcionais de árvores da Mata Atlântica do litoral do Paraná. O objetivo geral foi analisar padrões de diversidade e inferir processos de nicho responsáveis por variações na composição e riqueza de espécies arbóreas em escala local. A tese foi organizada em três capítulos: no primeiro, nós analisamos se os processos de nicho que determinam a diversidade beta de árvores variam de acordo com estágios de vida, grãos espaciais e pools de espécies. Nós encontramos que os processos variam com o estágio de vida em grãos finos, onde a diversidade beta de juvenis é afetada pela partição de recursos e a dos adultos, por competição. Porém, essas diferenças somem em grãos maiores, onde a competição determina a diversidade beta de ambos os estágios de vida. Diferenças no pool de espécies influenciam o padrão de agregação, mas não os processos que determinam a diversidade beta. No segundo capítulo, nós utilizamos uma abordagem funcional para analisar se diferenças na habilidade competitiva e os padrões de ocupação e preenchimento do espaço de nicho (volume funcional) influenciam a riqueza de espécies numa escala de vizinhança, em relação a diferentes tamanhos de pool de espécies. Concluímos que a competição deve ocorrer em algumas parcelas, mas não influencia o gradiente de riqueza. No entanto, à medida que as espécies são adicionadas à comunidade, em relação ao maior pool de espécies, são hermeticamente sobrepostas no espaço funcional, restrito pela filtragem ambiental, de modo que a filtragem ambiental é um processo dependente da escala responsável por gerar e manter a riqueza de espécies. No terceiro capítulo, partimos para uma abordagem metodológica com o objetivo de analisar o efeito do esforço amostral (número de unidades amostrais) em métricas de estrutura funcional (CWM e Rao) e na captura da resposta das espécies a gradientes ambientais. Nós encontramos que a composição funcional não foi afetada, mas a diversidade aumentou com a diminuição do esforço amostral, como um possível reflexo do aumento das diferenças funcionais entre espécies capturadas em menores amostragens. A resposta das espécies aos gradientes ambientais variou de acordo com o atributo considerado, sendo que, em geral, amostragens maiores apresentaram menos erros e foram, portanto, consideradas mais precisas. Em resumo, os resultados reforçam o papel dos processos de nicho em determinar a diversidade de árvores da Mata Atlântica e demonstram que o uso de diferentes abordagens pode ser crucial para englobar vários desses processos.



Palavras-Chave: Nicho. Filtragem ambiental. Exclusão competitiva. Partição de recursos. Diversidade funcional. Diversidade beta.

## ABSTRACT

One of the greatest challenges of ecology is to unravel the processes responsible for generating diversity patterns at different scales. This challenge becomes especially intriguing in highly biodiverse systems, such Brazilian Atlantic Forest. At local scales, niche processes (environmental filtering and biotic interactions) are expected to account for a large part of species composition and richness patterns. Thus, the use of different approaches that capture distinct aspects of the niche becomes fundamental to elucidate these processes. For this thesis, we performed an intensive sampling of species and functional traits of the Atlantic Forest trees at Paraná State coast. The general objective was to analyze diversity patterns and infer niche processes responsible for variations in the composition and richness of tree species on a local scale. The thesis was organized in three chapters: in the first, we analyzed whether the niche processes that determine the beta diversity of trees vary according to life stages, spatial grains and species pools size. We found that the processes differ for life stages in the fine grain, where the juvenile beta diversity is affected by the resource partitioning and adults beta diversity, by competition. However, these differences disappear in larger grains, where competition determines the beta diversity of both life stages. Differences in the species pool size influence the aggregation pattern, but not the processes that determine beta diversity. In the second chapter, we use a functional approach to analyze whether differences in competitive ability and occupancy and filling of the niche space influence the species richness on a neighborhood scale in relation to different species pool sizes. We conclude that competition should occur in some plots but does not influence the richness gradient. However, as species are added to the community, in relation to the largest species pool, they are hermetically overlaid in the functional space, restricted by environmental filtration, so that environmental filtering is a scale-dependent process responsible for generating the species richness gradient. In the third chapter, we use a methodological approach with the objective of analyzing the effect of sample effort (number of sample units) on functional structure metrics (CWM and Rao) and on the capture of species response to environmental gradients. We found that the functional composition was not affected, but the diversity increased with the reduction of the sampling effort, as a possible reflection of the increase of the functional differences between species captured in smaller samplings. The species response to environmental gradients varied according to the trait considered, and, in general, larger samplings presented lower errors and were therefore considered more accurate. In summary, the results reinforce the role of niche processes in determining the diversity of Atlantic Forest trees and demonstrate that the use of different approaches may be crucial to encompass several of these processes.



Keywords: Niche. Environmental filtering. Competitive exclusion. Resource partitioning. Functional diversity. Beta diversity.

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## 1. Introdução Geral

Desvendar os processos subjacentes à geração e manutenção da riqueza e diversidade de espécies em comunidades biológicas representa um dos maiores desafios da ecologia. Apesar disso, o crescente avanço nos estudos e teorias que remetem à montagem de comunidades e coexistência de espécies demonstra que esse desafio está longe de ser superado (MACARTHUR & LEVINS, 1967; DIAMOND, 1975; CONNOR & SIMBERLOFF, 1979; KEDDY, 1992; CHESSON, 2000; HUBBELL, 2001, MAYFIELD & LEVINE, 2010; HILLERISLAMBERS, 2012). É consenso que tais processos se vinculam às escalas temporais e espaciais em que ocorrem e imprimem padrões intrínsecos na comunidade os quais, quando analisados a partir de diferentes abordagens (em geral, taxonômicas, funcionais e filogenéticas) e confrontados com modelos nulos, ajudam a decifrar o processo predominante.

Do ponto de vista teórico, existe um quadro hierárquico que descreve as etapas do processo de montagem de comunidades desde a seleção de espécies a partir de um pool regional até a composição da comunidade local. Sumariamente, um pool regional, que é composto por um conjunto de espécies formado por processos de especiação, extinção e migração, definirá um pool local a partir da capacidade de dispersão das espécies; no local, a filtragem ambiental e as interações bióticas determinam a composição de comunidades (ZOBEL, 1997). Os processos compreendidos na montagem de comunidades podem ser agrupados em estocásticos (extinção, especiação, dispersão) e determinísticos (filtragem ambiental e limitação à similaridade), os quais, quando interagem entre si, determinam a dinâmica de comunidades.

Os processos estocásticos e determinísticos são tratados dentro dos arcabouços da teoria neutra (HUBBELL, 2001) e da teoria de nicho, respectivamente. A teoria neutra considera que a montagem de comunidades é regida essencialmente pelos processos de dispersão, especiação e extinção aleatórias, os quais independem das diferenças entre espécies (HUBBELL, 2001). Assim, toda espécie pode ser esperada para ocorrer em qualquer comunidade, o que gera padrões aleatórios. A montagem de comunidades sob

a óptica da teoria de nicho, por sua vez, se debruça sobre dois processos relacionados ao nicho: por um lado, a filtragem ambiental, que se refere ao conjunto de restrições abióticas ao estabelecimento das espécies em um local (KEDDY, 1992); por outro lado, a limitação à similaridade, que se refere às restrições bióticas na coexistência de espécies ecologicamente semelhantes (MACARTHUR & LEVINS, 1967). É esperado que os processos de nicho tenham muito mais força em escalas locais, e a compreensão do nicho como um hipervolume n-dimensional (HUTCHINSON, 1957), resultante de aspectos físicos e biológicos do ambiente que condicionam a existência de uma espécie, ajuda a entender a complexidade dos processos relacionados à montagem da comunidade final.

A filtragem ambiental é um dos mais notáveis conceitos em montagem de comunidades (KEDDY, 1992); refere-se a fatores abióticos que impedem o estabelecimento ou a persistência de espécies em um determinado local (KRAFT *et.al*., 2015). Em comunidades vegetais, a filtragem ambiental refere-se à germinação, estabelecimento e sobrevivência não aleatória de indivíduos com relação à variação nas características ambientais (KEDDY, 1992). É o filtro ao qual a espécie é submetida a partir do momento em que conseguiu se dispersar até o local, demonstrando que a capacidade de dispersão não é suficiente para a espécie compor a comunidade final. Devido à afinidade das espécies em tolerar as mesmas condições ambientais, comunidades estruturadas pela filtragem ambiental são caracterizadas por um conjunto de espécies que compartilham atributos ecológicos (KEDDY, 1992). Assim, a busca por um padrão de convergência fenotípica em dimensões ecológicas chave, em relação a uma expectativa nula, é a principal forma de testar a força da filtragem ambiental na assembleia de comunidades (WEIHER *et. al*., 1998; CORNWELL *et. al*., 2006; KRAFT *et. al*., 2008; SWENSON & ENQUIST, 2009). O sucesso diferencial das espécies também pode levar a mudanças na abundância (WHITTAKER, 1960), composição (KRAFT *et. al.*, 2011) e identidade funcional (CORNWELL & ACKERLY, 2009; SHIPLEY, 2009; SWENSON *et. al.*, 2012) de espécies em gradientes ambientais, outro conjunto de padrões que são frequentemente interpretados como evidência para filtragem ambiental.

A limitação à similaridade é baseada no pressuposto comum de que espécies ecologicamente semelhantes tendem a competir mais intensamente por recursos do que espécies diferentes e, portanto, são menos propensas a coexistir localmente (MACARTHUR & LEVINS, 1967). Por isso, no estudo de assembleias vegetais, a competição interespecífica tem recebido muito mais atenção e, provavelmente, é considerada a interação mais importante (KEDDY, 1989). Como o principal objetivo da competição na estrutura de comunidades é diminuir a sobreposição de nicho, estudos têm buscado evidências da competição a partir de padrões de divergência funcional, dispersão filogenética e diminuição na riqueza e similaridade na composição de espécies (WEBB *et. al.*, 2002; KRAFT & ACKERLY, 2010)

Os avanços mais recentes na teoria da coexistência têm evidenciado hipóteses sobre mecanismos implícitos na competição que, além de trazerem novas percepções, têm modificado a forma tradicional de associar os padrões aos seus respectivos processos. Uma dessas hipóteses é de que não apenas as diferenças de nicho, mas também as diferenças na habilidade competitiva das espécies determinam o resultado da competição (CHESSON, 2000). Assim, mecanismos estabilizadores de nicho fazem com que cada espécie se associe a um conjunto específico de recursos, aumentando a competição intraespecífica. Desse modo, competidores inferiores são poupados da exclusão competitiva pelos superiores (CHESSON, 2000; MAYFIELD & LEVINE, 2010; HILLERISLAMBERS *et al*., 2012). Por outro lado, a existência de diferenças hierárquicas nas habilidades competitivas leva à exclusão de competidores inferiores na ausência de segregação de nicho (CHESSON, 2000; MAYFIELD & LEVINE, 2010). Neste caso, a limitação interespecífica é maior do que a intraespecífica. Logo, para que os competidores inferiores se mantenham na comunidade, os mecanismos equalizadores de nicho devem amenizar essas diferenças e tornar a competição menos assimétrica (CHESSON, 2000, MAYFIELD & LEVINE, 2010, HILLERISLAMBERS *et. al.*, 2012).

A partição de recursos é vista como um dos principais mecanismos equalizadores de nicho. Ela ocorre quando as espécies diferem suficientemente na proporção no requerimento de seus recursos (TILMAN, 1982) e pode estabilizar a coexistência de espécies mesmo em um ambiente

espacialmente e temporalmente homogêneo; *trade-offs* nos requerimentos de recursos reduzem a sobreposição de nicho, enquanto as taxas de suprimento dos recursos influenciam as diferenças na habilidade competitiva (as espécies limitadas pelo recurso mais abundante terão uma vantagem competitiva) (ADLER *et. al.*, 2013). Nas comunidades de plantas terrestres, a tolerância à baixa disponibilidade de um recurso limitante é frequentemente um bom preditor de dominância competitiva (MILLER *et. al.*, 2005) e os *trade-offs* nos requerimentos de recursos podem promover a diversidade de espécies (HARPOLE & TILMAN, 2007).

É importante ressaltar que, quando há diferenças muito grandes na habilidade competitiva das espécies, a exclusão dos competidores inferiores e a manutenção de poucos competidores superiores podem resultar na diminuição da diversidade e num padrão de convergência fenotípica ou filogenética que pode ser confundida com a filtragem ambiental (MAYFIELD & LEVINE, 2010). Outra coisa importante, é que a heterogeneidade ambiental pode mediar a partição de nicho/recursos quando espécies diferentes são filtradas em diferentes pontos do gradiente (ADLER *et. al*., 2013). Assim, a filtragem ambiental contribui para padrões de divergência funcional, filogenética e para maior riqueza de espécies. Esses aspectos apenas reforçam a complexidade da interpretação dos processos que geram e mantêm a diversidade de espécies em comunidades biológicas.

## 1.2. Abordagens na investigação dos processos de montagem de comunidades

Entre as abordagens utilizadas na detecção dos processos de montagem de comunidades estão a diversidade beta taxonômica e a diversidade funcional. A diversidade beta taxonômica reflete a substituição de espécies no espaço e representa o quanto as diversidades de duas ou mais unidades espaciais diferem entre si (MAGURRAN, 2013). A substituição de espécies pode refletir processos determinísticos, como adaptações de espécies a diferenças de clima ou substrato, ou pode resultar de dispersão limitada acoplada a especiação, resposta tardia a mudanças climáticas ou outros processos históricos (CONDIT *et al*, 2002). Pode ser considerada tão

importante quanto a diversidade alfa para conservação, porque a substituição de espécies influencia a diversidade em grandes escalas (CONDIT *et.al*., 2002). Dentro desse contexto, abordagens envolvendo a diversidade beta e modelos nulos têm contribuído para gerar *insights* sobre importantes questões da ecologia, como o gradiente latitudinal de diversidade e a riqueza de espécies em sistemas altamente biodiversos (KRAFT *et. al.*, 2011).

A diversidade funcional compreende a diversidade de características ou atributos morfológicos das espécies que influenciam o funcionamento do ecossistema (TILMAN, 1986). Como a tolerância às condições ambientais e a habilidade para adquirir recursos são fatores determinados pelos atributos das plantas, a diversidade funcional se tornou, talvez, a principal abordagem para inferir processos de montagem de comunidades. Assim, mudanças nas médias de atributos chaves ligados à tolerância ambiental e obtenção de recursos, ao longo de diferentes gradientes (ambientais, bióticos) é ainda uma das principais formas de investigar o papel dos processos de nicho na montagem de comunidades (CORNWELL & ACKERLY, 2009). A posição de uma espécie em uma hierarquia de habilidades competitivas pode estar relacionada aos valores de seus atributos funcionais em comparação com outras espécies na comunidade, devido à ligação entre atributos e a capacidade de adquirir recursos limitantes (WESTOBY *et. al*., 2002). Aliado a este, o desenvolvimento de vários índices de diversidade funcional proporcionou a possibilidade de quantificar aspectos da complexidade do nicho multidimensional das espécies, como o total do espaço funcional preenchido pela comunidade (riqueza funcional) (MASON *et. al.*, 2005; VILLÉGER *et. al.*, 2008). Quantificar a forma como o espaço de nicho é ocupado e preenchido (através de métricas que determinam a distância funcional entre espécies dentro do espaço de nicho) ajuda a elucidar os processos relevantes da montagem de comunidades.

### 1.3. Mata Atlântica

A Mata Atlântica é um dos biomas mais singulares e ricos em biodiversidade do Brasil e é considerado um *hotspot* mundial (MYERS *et. al*., 2000). Estima-se que ela abriga mais de 25 mil espécies de diferentes grupos

taxonômicos; somente de plantas calcula-se que existam vinte mil espécies. Destas, oito mil são endêmicas e outras duzentas encontram-se ameaçadas de extinção (MINISTÉRIO DO MEIO AMBIENTE, 2010).

A Mata Atlântica estende-se por quase todo o litoral brasileiro, englobando quinze Estados da costa, mais alguns Estados do interior, como Minas Gerais e Piauí. Desde a costa até o interior do país, fatores climáticos delimitam pelo menos sete fitofisionomias da Mata Atlântica: formações pioneiras (incluindo manguezais e restingas), Floresta Ombrófila Densa, Floresta Ombrófila Aberta, Floresta Ombrófila Mista, Floresta Estacional Decidual, Floresta Estacional Semidecidual e Campos de Altitude (IBGE, 2012). A Floresta Ombrófila Densa, por exemplo, é caracterizada por um regime de chuvas intenso atrelado a temperaturas altas (25°C, em média) (MAACK, 2012). Em resposta a esses fatores climáticos predominam formas de vida macro e mesofanerófitas, lianas lenhosas e epífitas (IBGE, 2012).

Variações em escalas regionais na composição geológica, pedológica, na altitude e topografia do terreno definem cinco formações para a Floresta Ombrófila Densa: Aluvial (floresta ribeirinha), de Terras Baixas (planícies costeiras), Submontana (encostas de planaltos e/ou serras), Montana (no alto dos planaltos e/ou serras) e Alto-Montana (acima dos limites da formação Montana) (IBGE, 2012). Destas, a formação Submontana (~ 20 a 600 m a.n.m) é a que apresenta maior diversidade vegetal e complexidade estrutural. Uma parte disso é atribuída às propriedades de seus solos (em geral, Argissolos, Latossolos e Cambissolos), que são mais profundos e relativamente mais férteis. Outra parte é atribuída ao clima, caracterizado pela ausência de períodos de seca e de geadas. Na Floresta Ombrófila Densa submontana do litoral paranaense, ainda pode-se somar a estes fatores sua localização na transição entre a planície litorânea e a encosta da Serra do Mar (RODERJAN *et. al.*, 2002).

No sul do Brasil, a Floresta Ombrófila Densa submontana apresenta dossel multiestratificado, chegando a 30 m. Dentre as espécies que o caracterizam estão as pertencentes às famílias Lauraceae (*Ocotea catharinensis* Mez), Eleocarpaceae (*Sloanea guianensis* (Aubl.) Benth.), Fabaceae (*Schizolobium parahyba* (Vell.) S.F. Blake e *Pseudopiptadenia warmingii* (Benth.) G.P. Lewis & M.P. Lima), Myristicaceae (*Virola bicuhyba*

(Schott ex Spreng.) Warb.), Euphorbiaceae (*Alchornea triplinervia*), Phyllanthaceae (*Hyeronima alchorneoides* Allemao), Lecythidaceae (*Cariniana estrellensis* (Raddi) Kuntze) e Meliaceae (*Cabralea canjerana* (Vell.) Mart. e *Cedrela fissilis* Vell.). No sub-bosque, são comuns Rubiaceae (*Bathysa australis* (A.St.-Hil.) K.Schum., *Psychotria nuda* (Cham. & Schltdl.) Wawra e *Psychotria suterella* Müll. Arg.), Clusiaceae (*Garcinia brasiliensis* Mart.), Nyctaginaceae (*Guapira opposita* (Vell.) Reitz), Arecaceae (*Euterpe edulis* Mart.) e Cyatheaceae (*Cyathea hirsuta* C. Presl) (RODERJAN *et. al.*, 2002)

Como resultado de um cenário de exploração excessiva, a Mata Atlântica foi grandemente devastada. Desde a época da colonização europeia, os ciclos de exploração econômica e as expansões urbana e agroindustrial fizeram com que a vegetação natural da Mata Atlântica fosse reduzida drasticamente (FERRETI & BRITZ). Hoje, a maior parte da população brasileira (72%) vive em áreas de domínio da Mata Atlântica, que comporta, também, três dos maiores centros urbanos da América do Sul (MINISTÉRIO DO MEIO AMBIENTE, 2010). Esses dados dão uma dimensão da atual situação da Mata Atlântica em termos de conservação: apenas 12,4% da cobertura original do bioma de 1 milhão de Km persistem, sendo que, destes, 80% representam propriedades particulares (MINISTÉRIO DO MEIO AMBIENTE, 2010).

### 1.4. A Mata Atlântica no litoral do Paraná

A maior área contínua de Mata Atlântica do Brasil se encontra entre os litorais sul do Estado se São Paulo e norte do Estado do Paraná. Trata-se da região do Lagamar que é formada por um mosaico de estuários, manguezais, lagoas costeiras, rios litorâneos, restingas e florestas de planície e de montanha que comportam grande diversidade de espécies, das quais muitas são ameaçadas de extinção. Nesta região encontram-se diversas unidades de conservação, entre elas a APA de Guaraqueçaba, que inclui, entre outras, a Reserva Natural da Guaricica - RNG - (25º19'15"S, 45º42'24"W). A RNG é uma propriedade particular sob administração da Sociedade de Pesquisa em Vida Selvagem e Educação Ambiental (SPVS) que possui 8.600 hectares de Floresta Ombrófila Densa das subformações Aluvial, Terras baixas,

Submontana e Montana. Localiza-se no município de Antonina, litoral norte do Estado do Paraná.

O clima na região é do tipo Cfa na classificação de Köeppen, descrito como subtropical úmido mesotérmico, com verões quentes, sem estação seca e sem incidência de geadas (MAACK, 2012). Há influência, também, do tipo Cfb (clima oceânico, com precipitação bem distribuída ao longo do ano e verões mais frescos e úmidos) e Af, (clima equatorial, com temperatura e precipitação altas) (IPARDES, 2001). A temperatura média ao longo do ano é de 21,2 ºC. No mês mais quente (janeiro) a média é de 25,8 °C e no mês mais frio (junho) a média é de 16,4 °C. As temperaturas médias variam 9,4 °C ao longo do ano (FERRETI & BRITEZ, 2006). A precipitação média anual varia de 2.000 a 3.000 mm, com os maiores volumes de chuva ocorrendo no verão, nos meses de dezembro a março, sem períodos de seca (IPARDES, 2001).

Quatro classes de solos predominam na RNG e sua ocorrência está associada ao relevo; nas áreas mais planas ocorrem Neossolos e Gleissolos, enquanto os Cambissolos e Argissolos predominam nas áreas mais elevadas (FERRETTI & BRITEZ, 2006). Na área onde as parcelas para amostragem da vegetação foram instaladas ocorrem exclusivamente Cambissolos, caracterizados como solos minerais com horizonte B incipiente, pedogênese pouco avançada, e quantidade significativa de minerais primários e secundários em sua composição (MARTINS *et. al.*, 2015). Devido à heterogeneidade do material de origem, das formas de relevo e das condições climáticas, as características destes solos variam muito de um local para outro. Assim, a classe comporta desde solos fortemente até imperfeitamente drenados, de rasos a profundos, de cor bruna ou bruno-amarelada até vermelho escuro, e de alta a baixa saturação por bases (EMBRAPA, 2006)

A área que hoje inclui a RNG já sofreu com os impactos da exploração madeireira e extração do palmito (*Euterpe edulis*), mas, talvez, o impacto mais forte foi decorrente da criação de búfalos, que requeria grandes áreas desmatadas para cultivo de pastos (HÖFER *et. al.*, 2011). Com o abandono dessa atividade, ao longo dos anos, muitas destas áreas foram restauradas (FERRETTI & BRITEZ, 2006) e hoje compõem mosaicos de vegetação em diferentes estágios de sucessão.

## 1.5. Estrutura da Mata Atlântica na Reserva Natural da Guaricica

Apesar de um histórico de exploração da madeira e criação de búfalos que resultaram em mosaicos de vegetação em diferentes estágios de sucessão, a Reserva Natural da Guaricica ainda apresenta trechos muito bem conservados de FOD e alguns provavelmente intactos pelo Homem. A biodiversidade é surpreendente, sendo que um estudo anterior registrou mais de 300 espécies de árvores em diferentes estágios de sucessão numa área de 23 ha na reserva (BORGO *et. al*., 2011). No levantamento que propiciou esta tese, realizado numa área de 10 ha entre 2014 e 2017, foram registradas 252 espécies de árvores, três de palmeiras e oito de pteridófitas arborescentes, representando, em média, 104 espécies/ha. Estas foram distribuídas entre 140 gêneros de 59 famílias, das quais, se destacaram pela riqueza: Myrtaceae (35 spp), Fabaceae (33 spp), Rubiaceae (20 spp) e Lauraceae (16 spp). Estas famílias também se destacaram em diferentes subformações de Floresta Ombrófila Densa (GUILHERME *et. al.*, 2004; COLONETTI *et. al.*, 2009), o que ressalta sua importância para a caracterização geral desta subformação. A família Myrtaceae representa aproximadamente 13% do total de espécies na RNG e, devido à sua abundância e riqueza, é considerada uma das famílias mais características da FOD (PEIXOTO & GENTRY, 1990; TABARELLI & MANTOVANI, 1999; OLIVEIRA-FILHO & FONTES, 2000).

A estrutura horizontal da FOD na RNG é caracterizada, de maneira geral, pelas altas densidades relativas de *Euterpe edulis* e *Psychotria nuda*, e pela alta dominância relativa de *Sloanea guianensis*, *Hieronyma alchorneoides*, e *Alchornea triplinervia*. *E. edulis*, incluída na lista da flora brasileira ameaçada de extinção, é a espécie mais importante caracterizando a Floresta Ombrófila Densa da RNG e de diferentes regiões do Brasil devido sua alta densidade (COLONETTI *et. al.,* 2009; ROCHELLE *et. al.*, 2011). *P. nuda*, uma espécie de sub-bosque, é a segunda espécie mais importante da RNG, mas não aparece em estudos realizados em Santa Catarina (COLONETTI *et. al.*, 2009) e São Paulo (ROCHELLE *et. al.*, 2011) ou aparece com baixa importância para a comunidade (GOMES *et. al.*, 2011; RAMOS *et. al.*, 2011). A elevada densidade dessa espécie na área de estudo configura uma característica que diferencia a Floresta Ombrófila Densa Submontana da RNG de outras regiões do Brasil.

O estrato inferior da floresta na RNG é caracterizado por espécies de Rubiaceae (*Psychotria suterella* e *Psychotria nuda*) e Cyatheaceae (*Cyathea corcovadensis* (Raddi) Domin e *Cyathea leucopholis* Domin). O estrato intermediário é caracterizado por várias espécies de diferentes famílias, principalmente Myrtaceae, entre elas: *Marlierea obscura* O.Berg, *Myrcia spectabilis* DC. e *Marlierea tomentosa* Cambess. No estrato superior, se destacam: *Cryptocarya mandiocanna* Meisn. (Lauraceae), *Inga edulis* Mart (Fabaceae). e *Hieronyma alchorneoides* Allemão (Phylanthaceae).

Cerca de 30 % das espécies registradas neste levantamento são endêmicas da Mata Atlântica, como *Cryptocarya mandioccana* Meisn (Lauraceae) e *Campomanesia guaviroba* (DC.) Kiaersk (Myrtaceae); 12 % ocorrem apenas na subformação Floresta Ombrófila Densa (Stehmann et al., 2009), entre elas, *Tetrastylidium grandifolium* (Baill.) Sleumer (Olacaceae) e *Marlierea obscura* O.Berg (Myrtaceae). Pelo menos 8 % das espécies amostradas neste estudo estão sob alguma categoria de ameaça, algumas pela exploração excessiva, como é o caso de *E. edulis* (Arecaceae) e outras pela natureza rara, como *Ocotea catarinensis* (Lauraceae). O registro de ocorrência dessas espécies representa importante contribuição para a definição de seu estado atual de conservação e para o desenvolvimento de políticas de manejo e conservação.

## 1.6. O estudo, no contexto do PPBIO

O Programa de Pesquisa em Biodiversidade – PPBio – foi lançado em 2004 pelo Governo Federal e engloba diversas ações, desde o apoio a coleções biológicas, treinamento de taxonomistas, produção de guias de campo, pesquisas de campo e bioprospecção (PEZZINI *et. al*., 2011). Foi implantado primeiramente na Amazônia e depois se estendeu para outras regiões do Brasil e do mundo (Austrália e Argentina). Os projetos de pesquisa associados ao PPBio utilizam uma metodologia padronizada de amostragem que se aplica a diferentes grupos taxonômicos. Trata-se da metodologia RAPELD, cujo prefixo “RAP” se refere a avaliações rápidas e o sufixo “PELD”, se refere à sigla para “pesquisa ecológica de longa duração”. A proposta da

metodologia RAPELD é maximizar a probabilidade de amostrar adequadamente as comunidades biológicas e ao mesmo tempo minimizar a variação nos fatores abióticos que afetam estas comunidades (PEZZINI *et. al*., 2011). É uma metodologia baseada na proposta por Gentry e consiste em orientar o eixo maior das parcelas individuais ao longo da curva de nível do terreno, usando diferentes larguras de parcela para diferentes *taxa*, e distribuindo as parcelas regularmente através da paisagem a ser amostrada (MAGNUSSON *et. al,*, 2005).

Na Reserva Natural da Guaricica foi instalado um módulo RAPELD em área contínua de Floresta Ombrófila Densa Submontana (Figura 1). O módulo possui 5 km de comprimento por 1 km de largura e 10 parcelas de 1 ha com 1 km de distância uma da outra. Para a delimitação das parcelas, um corredor central de 1,5 m de largura e 250 m de comprimento foi demarcado seguindo a curva de nível do terreno, o que dá um aspecto irregular à parcela; Tomando como base a linha à montante que delimita o corredor central, foram definidas diferentes faixas de amostragem: faixa 1) possui 1.5 m de largura (faixa sensível) e foi usada para a amostragem de indivíduos juvenis, com diâmetro à altura do peito (DAP) de 1 a 4.9 cm; faixa 2) possui 20 m de largura, sendo 10 m para cada lado da linha do corredor central; esta faixa foi usada para amostrar indivíduos com DAP ≥ 5 cm; faixa 3) possui 40 m de largura, sendo 20 m para cada lado da linha à montante do corredor central; foi usada para amostrar indivíduos com DAP ≥ 10 cm. A parcela é subdividida em segmentos de 10 m de largura demarcados e identificados com o número da parcela e do segmento, assim cada parcela de 1 ha possui 25 segmentos, que são úteis como pontos de localização dentro da parcela para medidas das variáveis ambientais e mapeamento dos indivíduos arbóreos.

O módulo da RNG compreendeu um pequeno gradiente altitudinal, cuja parcela mais baixa (parcela 1) está a 23 m e a mais alta (parcela 9) está a aproximadamente 470 m a.n.m. As parcelas também diferem, em algum grau, no seu estágio de sucessão; três delas (parcelas 2, 4 e 8) se encontram em estágio médio enquanto as outras sete, em estágio avançado.

A amostragem da vegetação seguiu o protocolo do PPBio (disponível em: https://ppbio.inpa.gov.br/manuais). Em resumo, as plantas foram medidas nas diferentes faixas quanto ao seu DAP e altura, foram marcadas com tinta

permanente nos pontos onde o DAP foi medido e receberam uma plaqueta com número de identificação. Os indivíduos também foram mapeados com base em coordenadas x e y de localização dentro das parcelas. O material foi coletado e identificado em níveis de espécie e morfoespécies (Figura 1).

## 1.7. Objetivo

Esta tese teve como objetivo geral analisar padrões e inferir processos de nicho responsáveis por variações na composição e riqueza de espécies arbóreas da Mata Atlântica em escala local. A tese foi organizada em três capítulos: no primeiro, analisamos a relação entre diversidade beta de plantas juvenis e adultas com recursos do solo e perguntamos se os processos atuais que geram padrões de diversidade beta diferem ao longo da ontogenia e espacialmente de acordo com diferentes tamanhos de grãos espaciais e *pools* de espécies. No segundo, exploramos a relação entre competição, ocupação e preenchimento do espaço de nicho com a riqueza de espécies. No terceiro capítulo, avaliamos a influência do esforço amostral (número de unidades amostrais) na quantificação de duas importantes métricas de estrutura funcional das comunidades (CWM e Rao).

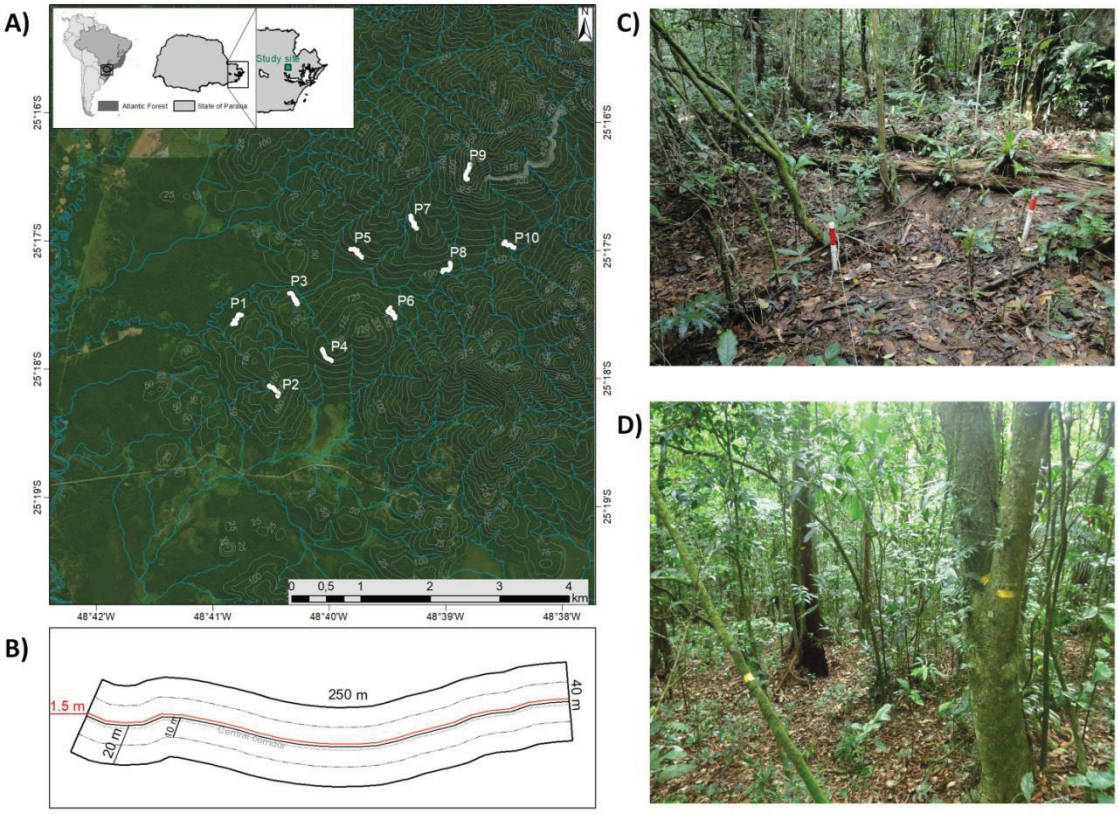


Figura 1 - Módulo RAPELD na Reserva Natural da Guaricica. A) Imagem de satélite indicando o local de instalação de cada parcela e a localização aproximada da Reserva. B) Esquema de uma parcela de 1 ha com suas respectivas faixas de amostragem. C) Interior de uma parcela com destaque para o corredor central. D) Interior de uma parcela com destaque para árvores amostradas e marcadas.

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# CAPÍTULO 1

## Contrasting community assembly mechanisms across tree life stages and at multiple spatial scales


### Abstract

Beta diversity, which measures variation in site-to-site species composition is an approach that, coupled with null models, can be useful to elucidate the processes responsible for generating diversity patterns in ecological communities. Given that community assembly processes may differ according to life stage, spatial grain and differences in the species pool size, accounting for these factors in the analysis becomes crucial to the understanding of its organization over time and space. In this study, we analyzed the beta diversity variation of trees in a mega-diverse tropical forest considering different life stages (juveniles and adults), spatial grains (fine and coarse) and species pool sizes (small, medium and large). We carry out an intensive sampling of trees on a local scale and explored through a null model if beta diversity patterns deviate from the expectation of stochastic assembly processes and were predicted by soil resource gradients. Our results indicate that juvenile communities are mostly affected by niche partitioning mediated by soil carbon, in the fine grain size, and by competitive exclusion, mediated by soil fertility, in the coarse grain size. We also found evidence that adult communities are mostly influenced by competitive exclusion mediated by phosphorus and soil fertility, and that this effect is pervasive spatially, across grain sizes and species pool sizes. We show that even in coarse spatial grain, the strength of biotic interactions may persist, contrary to what many studies indicate. Furthermore, our results demonstrate that juveniles can also be affected by this type of interaction and not only by dispersal limitation, environmental filtering or intraspecific competition, as the theory predicts. Variations in the species pool size do not always influence the processes that drive beta diversity in mega-diverse subtropical forests.

Keywords: Atlantic rainforest. Beta-diversity. Environmental filtering. Niche partitioning. Competitive exclusion.

## 1. Introduction

Elucidating the biotic and abiotic factors responsible for generating and maintaining species diversity at different scales remains a major challenge in community ecology. Among the approaches used for this purpose, beta diversity measures site-to-site variation in species composition, which results from individual responses of species to environmental gradients (COTTENIE, 2005; ANDERSON *et. al.*, 2011) and biotic interactions (e.g. competition; SEGRE *et. al.*, 2014). As species performance, environmental filtering and biotic interactions change along environmental gradients (KRAFT *et. al.*, 2015), beta diversity enable the investigation of the role played by niche process on community assembly (CONDIT *et. al.*, 2002; CHASE *et. al.*, 2011). However, since beta diversity is a simple function of alpha (local) and gamma (regional) diversities, the analysis of observed beta diversity only is not enough to infer assembly processes, since the sampling alone predicts changes in beta diversity caused simply by variations in the species pool sizes (sampling effect), which can generate non-random patterns in site-to-site composition leading to misinterpretations (CHASE & MYERS, 2011).

Approaches involving null models have been employed to distinguish the beta diversity variation from stochastic assembly processes (CHASE *et. al.*, 2011; CHASE & MYERS, 2011; KRAFT *et. al.*, 2011). Kraft *et. al.* (2011) used a null model that simulates processes of community assembly, which allows to evaluate the magnitude of beta diversity deviations from a null expectation based on a given species pool size. Significant deviations from the null expectation may reveal the main pattern of species dispersion in space, whether clustered or overdispersed (MYERS *et. al.*, 2013), since the degree of individual aggregation is crucial to the way a species uses resources and interacts with neighbors (CONDIT *et. al.*, 2000). In general, positive deviations may reflect intraspecific aggregation resulting from dispersal limitation or environmental filtering, negative deviations may reflect uniform distribution, and null deviations indicate random spatial distribution, probably related to stochastic processes (CHASE & MYERS, 2011; KRAFT *et. al.*, 2011; MYERS *et. al.*, 2013). However, there must be caution in interpretation, since different processes can generate similar patterns (CHASE & MYERS, 2011).

Although stochastic and niche processes may drive species distribution (QIAN & RICKLEFS, 2012), the strength of these processes may be related to spatial scale and grain size. We might expect that niche processes as environmental filtering and biotic interactions prevail at local scales (WEIHER & KEDDY, 1995) as plant species sorting is strongly determined by soil topographic and physicochemical variables (VALENCIA *et. al.*, 2004; BALDECK *et. al.*, 2012), which might influence both species tolerances and resource acquisition. The action of environmental filtering on species distribution at local scale is supported by studies showing non-random patterns of species-habitat association and species turnover along environmental gradients (SVENNING, 1999; WEBB & PEART, 2000). In addition, niche partitioning may be facilitated in heterogeneous environments, so that habitat heterogeneity may explain the coexistence of very different species (FANG *et. al.*, 2016). Since the role of biotic interactions on species distribution has received less attention, and although we know that other types of interaction influence the species distribution, most focus has been on how deterministic interspecific competition can homogenize communities diminishing the beta diversity (SEGRE *et. al.*, 2014).

As the niche requirement changes with ontogeny, the habitat associations and biotic interactions importance may change with the plant life stages (WEBB & PEART, 2000). Seedlings have dispersal limitation as a primary factor influencing their diversity (PAOLI *et. al.*, 2006); their spatial distribution is usually restricted to the proximity of parental individuals resulting in greater intraspecific aggregation (YANG *et. al.*, 2016) and consequently, greater beta diversity. However, evidence suggests that environmental filtering begins at early stages of plant development (BALDECK *et. al.*, 2012). The environment for juveniles is more finely heterogeneous than adults and they are more sensitive to this variation, presenting higher mortality rate than adults (WEBB & PEART, 2000). Thus, the regeneration niche would be responsible for determining much of the species distribution in communities in early life stages (QUERO *et. al.*, 2008; MARQUES & BURSLEM, 2015). Although environmental filtering is considered an important determinant of juvenile tree diversity, it does not exclude the importance of biotic interactions influencing its persistence (LIN *et. al.*, 2017). Because they are more spatially aggregated, seedlings generally

experience higher mortality rates than adults due to negative conspecific density dependence caused by pathogens or herbivores (COMITA *et. al.*, 2014), negative effects of conspecific neighbors (LIN *et. al.*, 2011) and potentially intraspecific competition for resources (TERBORG, 2012).

As the organism size increases, the demand for resources increases proportionally (WERNER & GILLIAN, 1984), and there is support for a hypothesis that biotic interactions increase their importance in later stages of development (KANAGARAJ *et. al.*, 2011; SWENSON, 2013). Many studies account for the role of self-thinning and density dependence in generating overdispersed patterns in late life stages (WRIGHT, 2002; GETZIN *et. al.*, 2006). Competition for limited resources should exclude individuals who are close neighbors, and restrict adult recruitment around other adult trees, resulting in a decrease in aggregation with the life stages (MURRELL, 2009). Although the effects of biotic interactions may prevail in late stages, environmental filtering also has potential to explain aggregate spatial distribution of adult trees (YANG *et. al.*, 2016). Thus, the adult assembly could be considered a reflection of intraspecific competition among juveniles, and the aggregate patterns in space of adult plants would show that competition is not the main factor acting on community assembly (GETZIN *et. al.*, 2006).

In general, studies evaluating the species-habitat association and the influence of assembly processes over ontogeny have found divergent results, since neutral processes (HU *et. al.*, 2012) and environmental filtering (PUNCHI-MANAGE *et. al.*, 2013) acting independently of life stages, until strong habitat associations observed exclusively for juveniles (KANAGARAJ *et. al.*, 2011) or adults (YANG *et. al.*, 2016) and dispersal limitation influencing juveniles only (YANG *et. al.*, 2016). There are no studies that analyze simultaneously ontogenetic responses at community level in highly biodiverse systems while use beta diversity as a tool to know processes that generate and maintain diversity along the ontogeny and in different grain sizes; yet, there are few studies that examine the influence of species pool size on beta diversity patterns (MYERS *et. al.*, 2013).

In this study, we asked whether current processes that generate beta diversity patterns in rainforest tree communities differ along ontogeny and spatially according different grain sizes and species pool sizes. To answer this

question, we assessed tree beta diversity in Brazilian Atlantic Forest – a mega-diverse tropical rainforest. We analyzed beta diversity of tree communities at the juvenile and adult life stages along an environmental resource gradient, and considering varying grain sizes and species pool sizes. As juveniles may be more sensitive to environmental variation, it is expected that their beta diversity is greater than adults and the processes that generate juveniles beta diversity patterns are related to abiotic filters (environmental filtering). On the other hand, as biotic interactions tend to be the main explanation for community structure at late stages of development and lose strength with increasing grain size, it is expected that density-dependent interactions (e.g. interspecific competition) will be more important for adults at small grain size while environmental filtering predominates in the large grain size.

## 2. Methods

### *2.1. Study area*

We carried out the study at the Guaricica Natural Reserve (25º19'15"S and 45º42'24"W), located in the municipality of Antonina, Paraná Sate, southern Brazil (Figure 1A). The Reserve has 8,600 ha and is included in the Guaraqueçaba Environmental Protection Area, one of the largest protected and continuous remnant areas of the Brazilian Atlantic Forest (FERRETTI & BRITEZ, 2006). The climate is subtropical humid mesothermal. The mean temperature is 21°C in the warmer months and 18°C in the colder months, with annual rainfall around 2,000 to 3,000 mm and relative air humidity around 85% (MAACK, 2012). The vegetation in the region is dominated by Submontane and Lowland Rainforests (IBGE, 2012). Forests are marked by three well defined strata, canopies of 20-30 m in height, and total tree species richness of more than 300 species (BORGO, 2011).

### *2.2. Sampling design and vegetation survey*

A RAPELD module has been established in a region of Submontane Rainforest in the reserve. RAPELD is a modification of the 0.1-hectare plot method developed by Alwyn Gentry and adapted to long-term ecological research sites that allow rapid inventories (MAGNUSSON *et. al.*, 2005). The RAPELD module consists of a set of ten 1-ha plots, systematically distributed in two rows with five plots, spaced 1 km from each other (Figure 1A). Each plot had 250 m long by 40 m wide and its center followed the ground level curve, minimizing internal variations in topography and soil. Altitude between plots ranged from 20 to 470 m a.s.l, while slope inclination ranged from 6° to 22°.

Vegetation survey was divided according to three plant size categories, using varying sampling ranges (Figure 1B): Sampling range 1 - Ranges 1.5-m wide , concentric with the 1-ha plot were used for sampling individuals with a diameter at breast height (DBH, 1.3 m) ≥ 1 cm (Figure 1B); Sampling range 2 - Ranges 20-m wide, also concentric with the 1-ha plot, were used for sampling individuals with DBH ≥ 5 cm (Figure 1B); Sampling range 3 – Ranges 40-m wide, representing the whole plot area, were used for sampling individuals with DBH ≥ 10 cm (Figure 1B). Individuals with DBH between 1 and 4.9 cm were considered juveniles and those with DBH ≥ 5 cm, adults. Individuals were identified at the species or morphospecies level.

To analyze possible variations in beta diversity according to grain size (i.e. the size of the individual sample units), juvenile and adult tree data were grouped into two spatial grain sizes (Figure 1C-D): 1) Fine grain: each 1-ha plot was divided into five subplots, with 50 m long and variable width according to plant life stage (Figure 1C). Then, we had fifty 75 $m^2$ subplots for juvenile individuals (50 m x 1,5 m) and fifty subplots with 2,000$m^2$ for adult individuals (50 m x 40 m); 2) Coarse grain: the spatial grain are the RAPELD module plots, totaling ten, which vary in size according to plant life stage (Figure 1D). In this extent, for juvenile individuals, we had ten plots with 375 $m^2$ and, for adult individuals, we had ten plots with 10,000 $m^2$ (250 m x 40 m). To calculate the observed beta diversity, we subdivided the plots into 10-m long and 1.5-m wide sections for juveniles, and 10-m long and 40-m wide for adults, totaling five sections for each fine grain (Figure 1C) and twenty five sections for each coarse grain (Figure 1D). We measured dissimilarity in species composition between sections within each fine or coarse grain using Jaccard index. The mean of

Jaccard dissimilarity was used as a measure of observed beta diversity for juveniles and adults at a given spatial grain size.

### *2.3. Environmental variables*

To evaluate the influence of the environment on the processes that regulate species beta diversity, we measured slope-, soil- and canopy-related environmental variables.

*Slope*: The slope within the plots in the RAPELD module was obtained with electronic tape and clinometer at georeferenced points and spaced 10 meters from each other, i.e., in each plot section. Slope was measured at four different points in each plot section. The four points mean was used as slope measure for each section. The slope value for each spatial grain, in turn, was represented by the mean of the angles obtained for the total sections composing the spatial grain (5 in small grain and 25 in large grain). As it was possible to measure the slope for each spatial grain section, we also calculated the variation coefficient of the means for each plot and subplot, which was used as estimate of heterogeneity for this environmental variable.

*Soil nutrients*: A simple soil sample was collected every 50 m of the plots in the RAPELD module, totaling five samples per plot. The samples were taken at depths of 0 to 5 cm, 5 to 10 cm, 10 to 20 cm and 20 to 30 cm. The samples were submitted to chemical analyses according to standardized methodology (Embrapa, 2006): pH (measured in $CaCl_2$), Phosphorus (P, mg/$dm^3$), Carbon (C, mg /$dm^3$), Calcium ($Ca^{2+}$, cmolc/$dm^3$), Magnesium ($Mg^{2+}$, cmol/$dm^3$), Sodium ($Na^+$, cmolc/$d^{m3}$), Potassium ($K^+$, cmol/$dm^3$), base sum (BS, cmolc /$dm^3$), base saturation (v,%), potential acidity ($H^+ + Al^{3+}$, cmolc/$dm^3$), Aluminum ($Al^{3+}$, cmolc /$dm^3$) and Aluminum saturation (m,%) (Appendix A1). Since the use of soil nutrients by plants occur in the first layers deep, we decided to use the soil average obtained at 0 to 20 cm depths. The raw values of soil chemical variables in 50 m were used to describe soil in the small grain; the mean values of five subplots described the soil in the large grain.

*Canopy opening*: The canopy opening was estimated using a spherical densiometer for each plot section. A reading was taken at about 1 m high, in the direction of each cardinal point, totaling four readings per section. The lighted

points reflected in the densiometer in each section for each cardinal point were summed. The average of these values multiplied by the correction factor 1.04 (LEMMON, 1956) represented the canopy opening percentage in fine grain (mean of 5 fractions) and coarse grain (mean of 25 fractions). The variation coefficient was also calculated for the canopy opening.

### 2.4. *Null model for beta diversity and statistical analyses*

To calculate the expected beta diversity, we used a null model that randomly sampled individuals from a previously defined species pool, but maintained the relative abundance of each species and the total number of individuals in each coarse or fine grain (KRAFT *et. al.*, 2011). The species pool is composed of species set capable of colonize a particular spatial grain. We consider three species pool size definitions: Small Pool) is composed of the total species registered within fine grains; Medium Pool) is composed of the total species registered within coarse grains; Large Pool) composed by the sum species in the RAPELD module. To account the species pools in calculating expected beta diversity in each spatial grain (fine and coarse) we did the following procedures (Figure 2):

1) Considering a given fine grain, we calculated its observed beta diversity; the expected beta diversity of this fine grain, in turn, was calculated based on: 1) the total number of species registered in the grain in question (small pool); 2) in the total number of species recorded in the 1-ha plot to which the fine grain belonged (medium pool); 3) in the total number of species recorded in the RAPELD module (large pool). This procedure was done for all 50 subplots that make up the fine grain.
2) Considering a given coarse grain, we calculate its observed beta diversity; their expected beta diversity was calculated based on: 1) the total number of species recorded within the 1-ha plot in question (medium pool); 2) in the total number of species recorded in the RAPELD module (large pool). This procedure was done for all 10 plots that make up the coarse grain.

To define the species pool, we took into account that in the study area even the longest distance between plots in RAPELD module (5 km) was not

large enough to prevent seed dispersal. We also took into account that juvenile community assembly should be influenced by the pool of adults but, as the environmental factors that influence juveniles at the present time may be different from those that influenced adults along their lives, we decided to keep the juvenile pool as composed only by juvenile species. We simulated community assembly 1000 times; the mean of beta diversity obtained after 1000 randomizations, with different pool sizes, represented the expected beta diversity for three different pool sizes: small, medium and large (Figure 2).

In order to analyze whether observed beta diversity differed from the null expectation, and whether such difference varied according to the pool size, we calculated the standardized effect size (SES) (GOTELLI, 2000). The SES, hereafter referred to as SES β, was computed as the observed beta diversity minus mean beta diversity of null communities, divided by the standard deviation of null communities. The SES β accounts for the influence of species pool on the observed beta diversity. A SES β closer to zero indicates that observed beta diversity does not differ from null expectation, whereas positive and negative values indicate higher (aggregate) and lower (uniform) beta diversity observed than expected at random, respectively. We calculated a SES β in relation to each pool size, which were named: SES $\beta_{small}$, SES $\beta_{medium}$ and SES $\beta_{large}$, calculated in relation to small, medium and large pools, respectively.

In order to test whether the observed beta diversity of juveniles and adults differed from one another in plots and subplots, we performed a *t*-test. To analyze whether environmental variables influenced local beta diversity, we performed the automatic selection of ordinary least squares (OLS) models using the Akaike information criterion (AICc, corrected for sample size) (BURNHAM & ANDERSON, 2004). The response variables were observed beta diversity and SES β, for fine and coarse grain and for juveniles and adults, in the three pool sizes. The normality of the response variables was evaluated graphically, from the frequency distribution, and tested using the Shapiro-Wilk test. To achieve normal distribution, some variables were submitted to transformation by positional normalization in range (coarse grain adults observed beta) and standardization (coarse grain adults SES $\beta_{medium}$). We used principal components analysis to guide the exclusion of collinear predictor variables, maintaining only representative variables of each variation axis (Appendix B1).

From a total of 16 environmental variables, six non-collinear variables of biological importance were selected and used in the subsequent analyses: 1) phosphorus (P) - compose key molecules such as nucleic acids, phospholipids and ATP and regulates important physiological processes for plants, such as photosynthesis and respiration; 2) carbon (C) - associated with the improvement of physical soil structure and C:N ratio; 3) base saturation percentage (v) - a variable that express soil fertility (Ca, K, Mg and Na percentage); 4) slope variation coefficient - express slope heterogeneity, which is indirect associate with soil resources and light availability; 5) canopy opening and 6) coefficient of variation (CV) of canopy opening - express light availability and light heterogeneity, respectively. Because light availability reaching the understory is largely influenced by the canopy, we included canopy openness (% and CV) as a predictor for analyses of juvenile data, but removed this variable from adult data.

The model selection was performed according to the following steps: first, a selection was made including all the predictor variables, which resulted in a list with several models. We selected those models that presented ΔAIC <2. Second, in order to avoid spatial dependence in the residuals (LEGENDRE & LEGENDRE, 1998), we tested for the spatial autocorrelation in the residuals of the selected models using Moran's I. Third, the models that presented spatial autocorrelation in residuals were submitted to new model selection including spatial filters as predictors variables to account for spatial autocorrelation. The spatial filters were obtained using the PCNM method (BORCARD & LEGENDRE, 2002) using a distance matrix, obtained from the sampling unit geographical coordinates (latitude and longitude). The geographical coordinates were used to calculate the truncation distance through the minimum spanning tree criterion (BORCARD & LENGENDRE, 2002). We used an algorithm that looked for the minimum set of spatial filters that accounted for the most of spatial autocorrelation in residuals (RANGEL *et. al.*, 2010). The predictor variables weights of the best models were used to explain the relationship of observed beta diversity and SES β with the environmental variables. Each model selection step was performed for juveniles and adults, in plots and subplots.

The beta diversity analyses, calculated through Jaccard dissimilarity, the null model and *t*-test were performed in R v.3.4.0 software (R CORE DEVELOPMENT TEAM, 2017). The principal component analyses, model selection and spatial autocorrelation were performed in SAM v. 4.0 software - Spatial Analyses in Macroecology (RANGEL *et. al.*, 2010).

## 3. Results

We recorded 162 species of juveniles and 223 species of adults in the RAPELD module. The fine grain was composed, in average, by 18 species of juveniles and 48 species of adults; the coarse grain was composed, in average, by 51 species for juveniles and 94 for adults.

Juveniles observed beta diversity was considerably larger than adults both in fine (Figure 3A, $t$ = 14.17, p <0.0001) and coarse grain (Figure 3B, $t$ = 10.05, p <0.0001). In the fine grain, β diversity ranged from aggregate to uniform, according to the species pool size, similarly for both life stages (Figure 4A and C). The SES $\beta_{small}$ is positive, indicating a trend towards intraspecific aggregation in species composition. The SES $\beta_{medium}$ is mostly negative and SES $\beta_{large}$ becomes totally negative, indicating the existence of a more uniform pattern of species composition variation (Figure 4A and C).

In the coarse grain, juvenile β diversity also varied in an aggregate and uniform way at the medium species pool (SES $\beta_{medium}$ 50% positive and 50% negative), while the in the large pool, the β diversity was totally uniform (SES $\beta_{large}$ totally negative) (Figure 4B). This demonstrates that there is a tendency for uniform distribution of juveniles as the species pool increases (Figure 4B). For adults in the coarse grain, SES $\beta_{medium}$ was mostly negative and SES $\beta_{large}$ was totally negative, showing that the general pattern of adult composition on this scale is uniform, regardless of the species pool size (Figure 4D).

Regarding the beta diversity relationship with environmental variables, in the fine grain, the juvenile β diversity was higher on soils with higher carbon (C) concentration (positive standardized regression coefficient for C, Table 1) (Appendix C1). The C was the variable that better explained the juveniles observed beta diversity, present in 90% of the models (Table 1), and the

juveniles SES β in the three pool sizes, present in 82, 76 and 90% of the models in small, medium and large species pools, respectively (Table 1). The other predictor variables were present between 24 to 38% of the models (Table 1). Variation in species composition was higher among adult communities on soils with lower concentration of phosphorus (P) (negative standardized regression coefficient for P, Table 1) (Appendix D1). The adults observed beta diversity was better explained by soil P, present in 72% of the models (Table 1). Similarly, soil P was important in explaining adult beta diversity, regardless of species pool size, as measured by SES β. This nutrient was present in 75, 95 and 75% of the models in the small, medium and large pools, respectively.

In the coarse grain, β diversity, both juveniles and adults, was higher in less fertile soils (negative standardized regression coefficient for v%, Table 1) (Appendix E1 – F1). The v% best explained the variation of observed beta diversity and SES β, for both juveniles and adults, in the medium and large pool analyzed, being present between 66 and 95% of the selected models. The other predictors were present between 10 to 27% of the models (Table 1).

## 4. Discussion

In general, we found that soil resources determine juvenile and adult beta diversity. While carbon and phosphorus determine the variation in juvenile and adult composition, respectively, in fine grain, soil fertility determines variation in juvenile and adult composition in the coarse grain. A general pattern we observed was of a more uniform variation in composition with the increase of the species pool. We also found that the pattern of variation of beta diversity was similar across the life stages and spatial grains.

### 4.1. *Beta diversity in Fine Grain*

For juveniles in the fine grain, we expected that environmental filtering predominate. We observed that variation in species composition was higher in Carbon rich soils, and that pattern of beta diversity variation was more aggregated in relation to small pool and became more uniform with the increase

in the pool size. Aggregate patterns of beta diversity variation can be attributed to environmental filtering or dispersal limitation (MYERS, 2013, KRAFT *et. al.*, 2011). Soil carbon, although not considered a very important resource for plants, can be associated with the improvement of soil structure, making it more porous, improving water infiltration and supply (KAY, 1998; SILVA & MENDONÇA, 2007), factors that can be determinant for the persistence of species in the habitat. However, the observed relationship between juvenile beta diversity and soil Carbon does not match to environmental filtering, since the higher intraspecific aggregation was observed in the Carbon richer soil.

Under Carbon richer soils, plants can produce abundant and extensive root systems that allow them to fetch water and other nutrients from the deeper layers of the soil (TISDALL & OADES, 1982). Since different species can be correlated to the same resource gradient, but differ in their responses to others resources (GILBERT & LECHOWICZ, 2004), the aggregate pattern of beta diversity variation can be attributed to species preference by different resources (TILMAN, 1982). Thus, we believe that soil Carbon can be mediate, at least in part, the resource partitioning between juveniles. Different studies has been show evidences for niche partitioning in the early plant life stages though the species-habitat association (KANAGARAJ *et. al.*, 2011; BALDECK *et. al.*, 2013). Differences in the distribution of soil resources make the environment more heterogeneous and facilitate coexistence by generating resource partitioning (ADLER *et. al.*, 2013). We observed that the resource partitioning process remained in relation to the medium species pool and intensified with the consideration of the large species pool. In fact, in the large species pool, juvenile beta diversity was larger and more uniform in Carbon rich soils. The uniform distribution in juvenile beta diversity indicates that the resources are likely to be used in a similar way avoiding the negative effects of competition, which should favor the coexistence of a greater number of juvenile species.

Others studies indicate that the dispersion limitation is an important factor in the juveniles distribution (HU *et. al.*, 2012, YANG *et. al.*, 2016). Thus, we believe that the dispersion limitation acts upon establishment of the plant on site, i.e. at the time of germination and early seedling days of life. Soon after its germination, the seedling begins to suffer with effects in the abiotic and biotic environment and, in the subsequent stages of development, these effects tend

to be more evident. The juveniles of our study (DAP 1 to 4.9 cm) cannot be considered seedlings in a way that we believe that niche partitioning mediated by soil Carbon are plausible processes to explain diversity at this stage of development.

In relation to the adults in the fine grain, we expected that the biotic interactions would be very important. We observed that the variation in their composition was lower in phosphorus rich soils, regardless pool size. However, the variation pattern was aggregated in relation to small pool, but this aggregation was less intense in phosphorus rich soils. This pattern probably reflects that the adult species compete in phosphorus poor soil and the heterogeneity in the distribution of this resource favored the aggregate pattern of variation. However, as the concentration of phosphorus in the soil increases, the lower observed beta diversity and the less aggregate pattern of beta diversity variation indicate that in these environments, probably, the species have experienced, greater intensity, the competitive exclusion that defined the current species composition in soils rich in phosphorus.

The soil phosphorus is an important resource known to limit productivity in terrestrial environments (ELSER *et. al.*, 2007) and influence biotic interactions such as competition (TILMAN, 1986). Thus, this relationship must be an indication that species more limited by phosphorus were excluded, by competition, by species with the lowest requirement of this resource (ADLER, 2013). This agrees with the hypothesis that more fertile environments are expected to exhibit less diversity because high growth rates of certain species allow competitive exclusion to occur rapidly (HUSTON, 1979). Thus, if two species compete for a particular resource, the species with the least requirement of this resource should displace the other, as this may reduce the resource below the level required to maintain the species with the highest requirement (TILMAN, 1986). Increasing any resource result in fewer species with better competitive ability coexisting and consequently decreasing beta diversity in more resource rich soils (HARPOLE & TILMAN, 2007; SEGRE *et. al.,* 2014). This result is consistent with Segre (2014) removal experiments who found decrease in beta diversity with increased interspecific competition.

In response to the increase in the species pool size, variation in adult species composition remained low in phosphorus rich soils, but the pattern of

adult beta diversity variation was no longer aggregated and became uniform. In fact, the more uniform pattern of beta diversity variation should reflect that resource partitioning predominates at this life stage. However, competition for limited resources influences the exclusion of individuals who are close neighbors and restrict the recruitment of adults around other adult trees (MURRELL, 2009). This process is known to generate less aggregate patterns of species distribution (MURRELL, 2009). This reinforces the importance of competitive exclusion in determining adult beta diversity and should also indicate that among these dominant species and competitively superior, resource utilization is made equally, given its uniform pattern of variation.

### *4.2 Beta Diversity in Coarse grain*

In this grain, our hypotheses were that the environmental filtering would predominate for juveniles and adults. We found that both juveniles and adults beta diversity (observed and SES β) was negatively related to soil fertility, as measured by base saturation (v %). In other words, species composition is low variable in more fertile soils. We also found that in the medium pool, the juvenile beta diversity varies from aggregate to uniform in the same proportion (50% of the plots for each pattern) whereas the adults beta diversity varies predominantly uniformly towards the most fertile end of the gradient.

Some degree of intraspecific aggregation is observed in less fertile soils for both life stages. However, the predominant pattern is of lower variation in species composition in more fertile soils, accompanied by a more uniform variation in species composition. This pattern, in general, reflects that the same processes influenced adult beta diversity in fine grain regarding medium and large species pool probably influences juvenile and adult beta diversity in coarse grain. Thus, we believe that the competitive exclusion of species that require more fertile soils to settle and grow predominates in the coarse grain, especially among adults.

For us, this result is surprising because the spatial scale at which the data were analyzed should favor capture of environmental filtering. In other studies, environmental filtering has been evoked to explain this same pattern (LALIBERTÉ *et. al.*, 2014; ZEMUNIK *et. al.*, 2016). According to this view, the

regional pool is composed of many species adapted to less fertile environments that are more favored in the poor end of the gradient (LALIBERTÉ *et. al.*, 2014). Despite our expectation, we believe that the poor soil characteristics of the study area, typical in tropical forests, does not represent an environment as extreme as that observed in the dunes (LALIBERTÉ *et. al.*, 2014; ZEMUNIK *et. al.*, 2016), which may not represent such a strong environmental filter as well as being a relatively short gradient. Thus, we judge that, surprisingly, competitive exclusion to be the best explanation for the decrease in beta diversity of both life stages in large grain in relation to increase in soil fertility in our study.

### *4.3 Relationship between beta diversity, grain size and pool size*

The pattern observed in the beta diversity corroborated part of our hypothesis regarding the fine grain, but it differed from our expectation in coarse grain. In the fine grain size, we believe that capture of niche partitioning for juveniles and competitive exclusion for adults can be an effect of the better resolution of the explanatory variables obtained in the fine grain, that is, the heterogeneity of the soil chemical variables. With the increase of grain size we expected greater influence of environmental filtering (WEIHER & KEDDY, 1995) for both juveniles and adults. Unlike our expectations, we found that competitive exclusion probably predominates in coarse grain for both life stages. This was particularly surprising for juveniles, since competition is an interaction that may influence species distribution at this life stage, but is usually intraspecific given the aggregation of individuals close to the parent plant (COMITA *et. al.*, 2014). However, as juveniles are in transition to the adult life stage, interspecific competition may begin to have an effect on their beta diversity. We also believe that juveniles beta diversity is greater than adults when competitive exclusion predominates in large grain because juveniles, besides facing the effects of competition, are more sensitive to environmental variations and consequently their greater beta diversity may result of the two processes acting together. Our results highlight the importance of considering grain size when analyzing patterns of species diversity.

Variations in the species pool size did not influence the relationship of beta diversity to environmental variables, either juveniles or adults, and in no

grain size, but influenced the variation pattern of beta diversity in general, ranging from aggregate to uniform with increase in the species pool size. Our results indicate that, even with differences in variation pattern of beta diversity, variations in the species pool size do not alter the processes that generate the patterns observed in beta diversity in general.

## 5. Conclusion

We conclude that there are differences in the processes that drive beta diversity through life stages, but these differences tend to disappear with increasing spatial grain. In coarse grain we observed interspecific competition influence on the beta diversity of both juvenile and adult life stages, which is a surprising finding compared to that expected in the literature (WEIHER & KEDDY, 1995) especially to juveniles, for which it expects stronger influence of dispersal limitation (YANG *et. al.*, 2016.), environmental filtering (KANAGARAJ *et. al.*, 2011; BALDECK *et. al.*, 2012) or intraspecific competition (TERBORG, 2012). In addition, we found that variations in the species pool size influence in beta diversity patterns but not in the processes that generate these patterns on a local scale, differently from what is expected (KRAFT *et. al.*, 2011). This result demonstrates the importance of dissociating the simple observation patterns from their generating processes in the community assembly context.

## 6. References

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Table 1. Weight of predictor variables present in the selected models with delta AICc <2 and their respective standardized regression coefficients. AW = Akaike weight; Std. Coeff = Standardized coefficient. In bold, the most important predictor variables.

| Sampling unit grain | Life stage | Response variable | Carbon | | Phosphorous | | Base saturation | | Canopy openness | | Canopy openness variation | | Slope variation | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | AW | Std. Coeff. | AW | Std. Coeff. | AW | Std. Coeff. | AW | Std. Coeff. | AW | Std. Coeff. | AW | Std. Coeff. |
| Coarse | Juveniles | Observed β diversity | 0.21 | 0.49 | 0.26 | -0.44 | **0.69** | -0.72 | 0.09 | 0.33 | 0.06 | 0.00 | 0.05 | -0.01 |
| | | SES $\beta_{medium}$ | 0.18 | 0.32 | 0.11 | -0.31 | **0.66** | -0.69 | 0.07 | 0.11 | 0.13 | 0.36 | 0.09 | -0.23 |
| | | SES $\beta_{large}$ | 0.22 | 0.50 | 0.28 | -0.45 | **0.67** | -0.71 | 0.09 | 0.34 | 0.06 | 0.00 | 0.05 | -0.02 |
| | Adults | Observed β diversity | 0.20 | 0.18 | 0.07 | -0.04 | **0.80** | -0.74 | - | - | - | - | 0.23 | 0.40 |
| | | SES $\beta_{medium}$ | 0.87 | -1.46 | 0.06 | -0.38 | **0.96** | -1.78 | - | - | - | - | 0.09 | 0.44 |
| | | SES $\beta_{large}$ | 0.20 | 0.26 | 0.07 | -0.07 | **0.79** | -0.72 | - | - | - | - | 0.19 | 0.37 |
| Fine | Juveniles | Observed β diversity | **0.90** | 0.36 | 0.26 | -0.07 | 0.25 | -0.06 | 0.24 | -0.03 | 0.34 | -0.14 | 0.30 | 0.11 |
| | | SES $\beta_{small}$ | **0.82** | 0.32 | 0.38 | -0.16 | 0.25 | -0.04 | 0.26 | -0.06 | 0.26 | -0.07 | 0.24 | -0.02 |
| | | SES $\beta_{medium}$ | **0.76** | 0.30 | 0.25 | 0.02 | 0.25 | 0.01 | 0.26 | -0.05 | 0.32 | -0.12 | 0.36 | 0.15 |
| | | SES $\beta_{large}$ | **0.90** | 0.36 | 0.26 | -0.07 | 0.25 | -0.06 | 0.24 | -0.03 | 0.35 | -0.15 | 0.30 | 0.11 |
| | Adults | Observed β diversity | 0.34 | 0.14 | **0.72** | -0.26 | 0.24 | -0.06 | - | - | - | - | 0.38 | 0.15 |
| | | SES $\beta_{small}$ | 0.23 | 0.03 | **0.75** | -0.28 | 0.34 | -0.14 | - | - | - | - | 0.37 | 0.15 |
| | | SES $\beta_{medium}$ | 0.28 | 0.10 | **0.95** | -0.39 | 0.25 | -0.06 | - | - | - | - | 0.27 | 0.09 |
| | | SES $\beta_{large}$ | 0.35 | 0.14 | **0.75** | -0.27 | 0.24 | -0.05 | - | - | - | - | 0.38 | 0.15 |

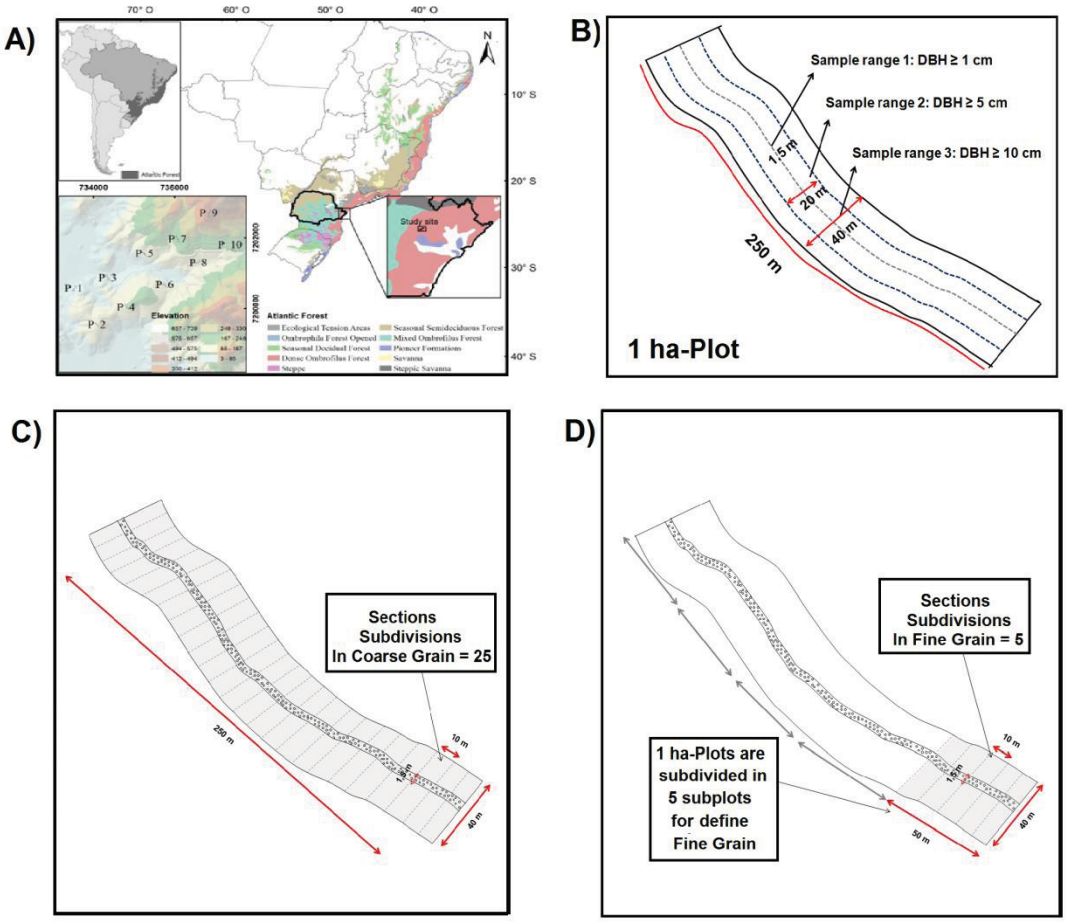



Figure 1 - Scheme of the sample design. A) location of the study area with highlight to the RAPELD module; B) scheme of a 1-ha plot with their respective sampling ranges; C) scheme of a large grain and its subdivision into sections; D) scheme of a small grain and its subdivision into sections.

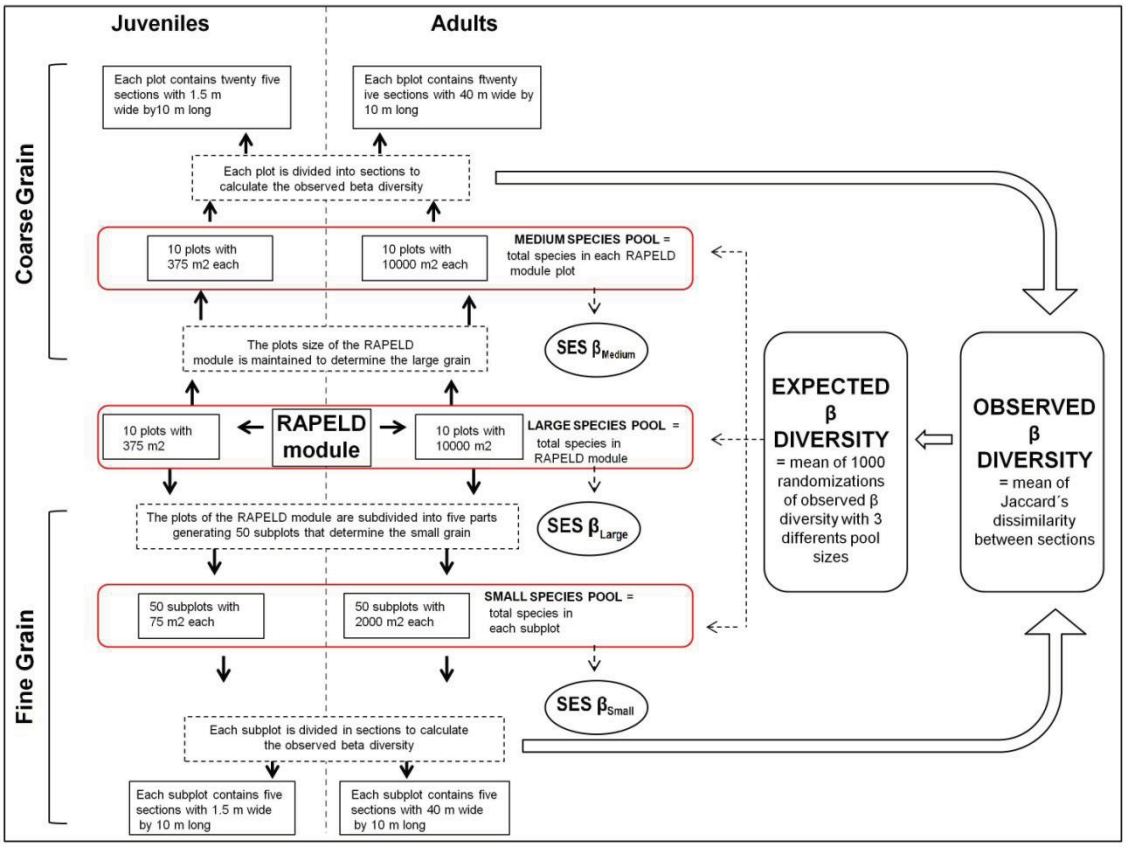



Figure 2. Scheme of the analytical procedure used for the spatial grains definition, beta diversity and standardized effect size measures.

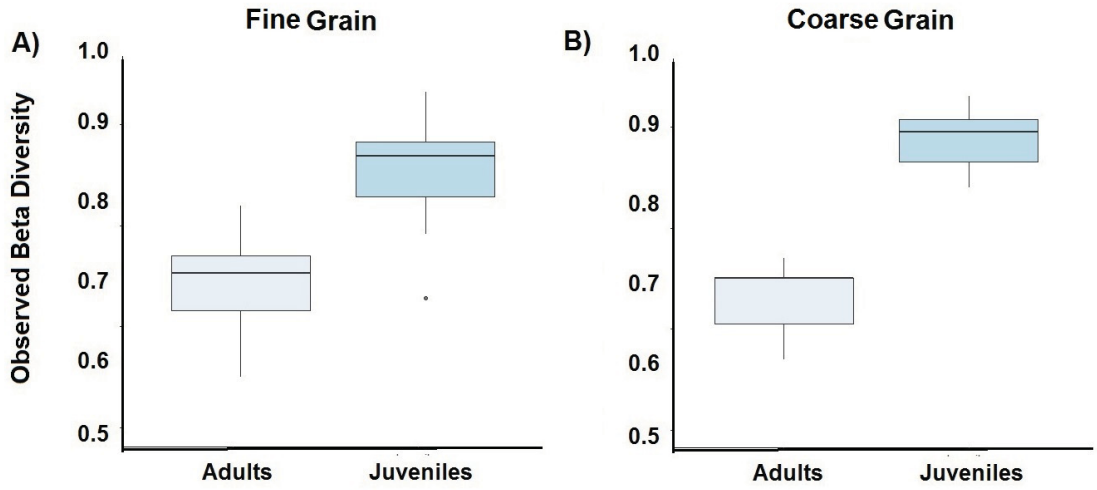



Figure 3. Differences in observed beta diversity for: A) adults and juveniles in fine grain; B) adults and juveniles in coarse grain.

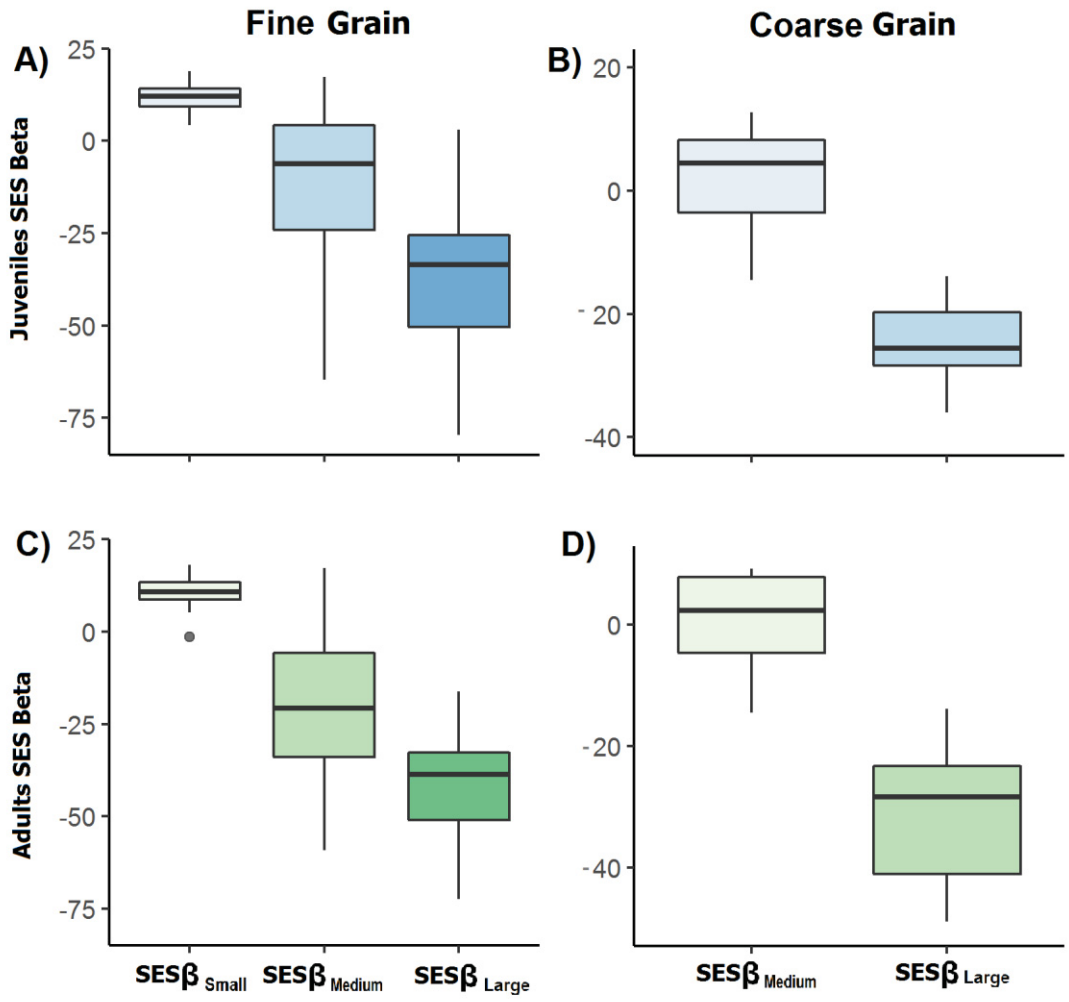



Figure 4. Standardize effect size for beta diversity (SES β) with three pool sizes for juveniles and adults in different grain sizes. A) Juveniles in fine grain; B) Juveniles in coarse grain; C) Adults in fine grain; D) Adults in coarse grain. $SES_{small}$, $SES_{medium}$ and $SES_{large}$ refer to small species pool (species fine grain), medium pool (species in 1-ha coarse grain) and pool 3 (total species in RAPELD module), respectively.

## 7. APPENDICES

**Appendix A1** – Mean and standard deviation of soil chemical variables collected in the plots of the RAPELD module. The values on grey lines represent the mean and standard deviation (SD) of the soils values obtained for each coarse grain (1-ha plot). The values on white lines represent the raw soil values obtained in each fine grain (200 $m^2$ subplot).

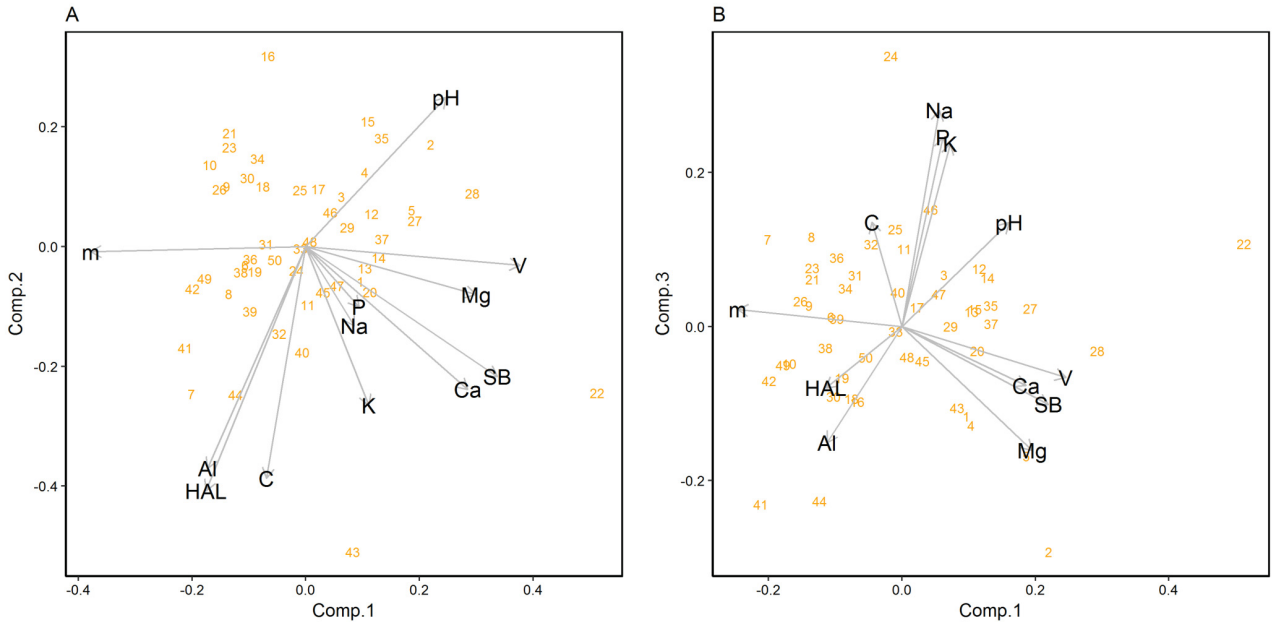
| Spatial Grain | pH CaCl2 | | Al cmolc/dm³ | | H+AL cmolc/dm³ | | Ca cmolc/dm³ | | Mg cmolc/dm³ | | Na cmolc/dm³ | | K cmolc/dm³ | | SB cmolc/dm³ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| COARSE_1 | 3.83 | *0.15* | 2.47 | *0.49* | 10.57 | *3.04* | 0.50 | *0.14* | 0.49 | *0.32* | 0.04 | *0.02* | 0.10 | *0.03* | 1.12 | *0.47* |
| FINE_1.1 | 3.80 | *0.13* | 3.11 | *0.30* | 11.83 | *1.59* | 0.57 | *0.22* | 0.47 | *0.31* | 0.03 | *0.01* | 0.12 | *0.05* | 1.20 | *0.57* |
| FINE_1.2 | 4.00 | *0.04* | 2.30 | *0.72* | 11.26 | *1.96* | 0.50 | *0.20* | 0.72 | *0.32* | 0.02 | *0.00* | 0.08 | *0.04* | 1.33 | *0.56* |
| FINE_1.3 | 3.97 | *0.09* | 2.47 | *0.60* | 11.14 | *1.95* | 0.46 | *0.07* | 0.27 | *0.07* | 0.03 | *0.01* | 0.10 | *0.03* | 0.86 | *0.18* |
| FINE_1.4 | 3.70 | *0.04* | 2.23 | *0.29* | 6.68 | *5.81* | 0.49 | *0.16* | 0.41 | *0.23* | 0.04 | *0.01* | 0.09 | *0.03* | 1.03 | *0.43* |
| FINE_1.5 | 3.69 | *0.05* | 2.23 | *0.23* | 10.84 | *1.45* | 0.47 | *0.17* | 0.68 | *0.55* | 0.05 | *0.03* | 0.10 | *0.03* | 1.31 | *0.78* |
| COARSE_2 | 3.64 | *0.15* | 2.74 | *0.55* | 12.87 | *2.96* | 0.22 | *0.05* | 0.16 | *0.11* | 0.04 | *0.02* | 0.12 | *0.04* | 0.54 | *0.14* |
| FINE_2.1 | 3.55 | *0.08* | 2.82 | *0.41* | 12.69 | *1.47* | 0.19 | *0.04* | 0.28 | *0.17* | 0.04 | *0.02* | 0.14 | *0.06* | 0.66 | *0.26* |
| FINE_2.2 | 3.43 | *0.13* | 3.53 | *0.77* | 17.09 | *4.29* | 0.21 | *0.09* | 0.19 | *0.11* | 0.05 | *0.03* | 0.13 | *0.03* | 0.57 | *0.17* |
| FINE_2.3 | 3.59 | *0.06* | 2.93 | *0.28* | 12.50 | *1.32* | 0.25 | *0.09* | 0.14 | *0.08* | 0.05 | *0.01* | 0.13 | *0.04* | 0.57 | *0.08* |
| FINE_2.4 | 3.78 | *0.10* | 2.24 | *0.32* | 12.47 | *3.47* | 0.21 | *0.04* | 0.14 | *0.09* | 0.03 | *0.01* | 0.09 | *0.04* | 0.47 | *0.11* |
| FINE_2.5 | 3.68 | *0.01* | 2.53 | *0.14* | 11.04 | *1.57* | 0.22 | *0.03* | 0.11 | *0.07* | 0.03 | *0.02* | 0.08 | *0.06* | 0.44 | *0.08* |
| COARSE_3 | 3.81 | *0.18* | 2.19 | *0.39* | 11.70 | *1.86* | 0.34 | *0.22* | 0.42 | *0.28* | 0.05 | *0.02* | 0.12 | *0.04* | 0.92 | *0.50* |
| FINE_3.1 | 3.63 | *0.16* | 2.80 | *0.26* | 13.29 | *1.28* | 0.42 | *0.23* | 0.31 | *0.32* | 0.05 | *0.02* | 0.14 | *0.06* | 0.91 | *0.59* |
| FINE_3.2 | 3.80 | *0.04* | 2.17 | *0.06* | 11.55 | *0.82* | 0.46 | *0.07* | 0.38 | *0.17* | 0.05 | *0.01* | 0.11 | *0.04* | 1.01 | *0.28* |
| FINE_3.3 | 3.62 | *0.07* | 2.43 | *0.21* | 12.37 | *0.74* | 0.39 | *0.07* | 0.52 | *0.19* | 0.07 | *0.03* | 0.13 | *0.06* | 1.10 | *0.22* |
| FINE_3.4 | 3.91 | *0.15* | 2.17 | *0.06* | 11.44 | *1.64* | 0.32 | *0.42* | 0.60 | *0.50* | 0.04 | *0.01* | 0.12 | *0.05* | 1.08 | *0.97* |
| **Spatial Grain** | **pH CaCl2** | | **Al cmolc/dm³** | | **H+AL cmolc/dm³** | | **Ca cmolc/dm³** | | **Mg cmolc/dm³** | | **Na cmolc/dm³** | | **K cmolc/dm³** | | **SB cmolc/dm³** | |

| | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| FINE_3.5 | 4.02 | *0.10* | 1.75 | *0.14* | 9.36 | *2.84* | 0.20 | *0.16* | 0.50 | *0.23* | 0.05 | *0.01* | 0.09 | *0.03* | 0.83 | *0.42* |
| COARSE_4 | 3.72 | *0.16* | 2.31 | *0.61* | 11.48 | *1.72* | 0.29 | *0.22* | 0.44 | *0.28* | 0.04 | *0.01* | 0.11 | *0.04* | 0.89 | *0.53* |
| FINE_4.1 | 3.81 | *0.09* | 1.73 | *0.17* | 9.52 | *1.41* | 0.13 | *0.04* | 0.28 | *0.23* | 0.04 | *0.02* | 0.07 | *0.04* | 0.51 | *0.32* |
| FINE_4.2 | 3.83 | *0.06* | 1.93 | *0.19* | 10.87 | *0.40* | 0.25 | *0.16* | 0.36 | *0.22* | 0.03 | *0.01* | 0.12 | *0.04* | 0.76 | *0.43* |
| FINE_4.3 | 3.62 | *0.16* | 2.33 | *0.16* | 12.17 | *1.94* | 0.27 | *0.18* | 0.30 | *0.23* | 0.03 | *0.01* | 0.09 | *0.03* | 0.69 | *0.44* |
| FINE_4.4 | 3.55 | *0.20* | 3.09 | *0.31* | 13.66 | *1.33* | 0.15 | *0.11* | 0.46 | *0.35* | 0.05 | *0.01* | 0.11 | *0.03* | 0.77 | *0.49* |
| FINE_4.5 | 3.67 | *0.09* | 2.64 | *0.96* | 12.12 | *1.19* | 0.45 | *0.32* | 0.54 | *0.33* | 0.04 | *0.01* | 0.13 | *0.03* | 1.17 | *0.66* |
| COARSE_5 | 3.88 | *0.16* | 2.06 | *0.58* | 11.47 | *1.46* | 0.38 | *0.49* | 0.33 | *0.29* | 0.06 | *0.03* | 0.12 | *0.04* | 0.89 | *0.75* |
| FINE_5.1 | 3.73 | *0.13* | 1.54 | *0.43* | 12.17 | *0.96* | 0.07 | *0.07* | 0.19 | *0.15* | 0.03 | *0.01* | 0.09 | *0.03* | 0.38 | *0.25* |
| FINE_5.2 | 4.08 | *0.04* | 2.26 | *0.73* | 10.76 | *0.41* | 1.34 | *0.35* | 0.55 | *0.12* | 0.07 | *0.02* | 0.15 | *0.04* | 2.11 | *0.49* |
| FINE_5.3 | 3.91 | *0.05* | 2.83 | *0.30* | 9.86 | *0.87* | 0.15 | *0.07* | 0.12 | *0.07* | 0.03 | *0.01* | 0.10 | *0.02* | 0.40 | *0.16* |
| FINE_5.4 | 3.80 | *0.08* | 1.92 | *0.50* | 12.76 | *1.08* | 0.11 | *0.03* | 0.25 | *0.08* | 0.11 | *0.02* | 0.15 | *0.06* | 0.62 | *0.18* |
| FINE_5.5 | 3.84 | *0.03* | 1.63 | *0.31* | 12.47 | *0.79* | 0.22 | *0.13* | 0.26 | *0.17* | 0.05 | *0.01* | 0.12 | *0.04* | 0.64 | *0.34* |
| COARSE_6 | 3.78 | *0.19* | 2.39 | *0.45* | 11.20 | *1.61* | 0.37 | *0.27* | 0.35 | *0.26* | 0.04 | *0.02* | 0.13 | *0.04* | 0.89 | *0.53* |
| FINE_6.1 | 3.70 | *0.11* | 2.53 | *0.48* | 12.01 | *2.37* | 0.07 | *0.08* | 0.21 | *0.13* | 0.03 | *0.01* | 0.13 | *0.05* | 0.45 | *0.27* |
| FINE_6.2 | 3.92 | *0.09* | 2.10 | *0.20* | 10.16 | *1.23* | 0.52 | *0.48* | 0.48 | *0.32* | 0.04 | *0.00* | 0.14 | *0.05* | 1.18 | *0.84* |
| FINE_6.3 | 4.07 | *0.06* | 2.08 | *0.52* | 9.62 | *0.27* | 0.50 | *0.36* | 0.67 | *0.32* | 0.04 | *0.01* | 0.14 | *0.06* | 1.34 | *0.75* |
| FINE_6.4 | 3.72 | *0.09* | 2.10 | *0.38* | 11.55 | *0.78* | 0.42 | *0.20* | 0.37 | *0.16* | 0.04 | *0.01* | 0.13 | *0.02* | 0.95 | *0.38* |
| FINE_6.5 | 3.56 | *0.14* | 2.62 | *0.38* | 11.55 | *1.62* | 0.35 | *0.03* | 0.15 | *0.06* | 0.03 | *0.00* | 0.10 | *0.03* | 0.63 | *0.11* |
| COARSE_7 | 3.80 | *0.12* | 2.38 | *0.60* | 11.98 | *3.68* | 0.29 | *0.22* | 0.31 | *0.18* | 0.04 | *0.01* | 0.12 | *0.05* | 0.76 | *0.41* |
| FINE_7.1 | 3.80 | *0.15* | 2.82 | *0.60* | 11.95 | *1.81* | 0.32 | *0.08* | 0.19 | *0.11* | 0.04 | *0.01* | 0.12 | *0.05* | 0.67 | *0.25* |
| FINE_7.2 | 3.79 | *0.10* | 2.93 | *0.45* | 16.57 | *7.73* | 0.35 | *0.36* | 0.26 | *0.14* | 0.05 | *0.01* | 0.14 | *0.06* | 0.80 | *0.57* |
| FINE_7.3 | 3.76 | *0.09* | 2.72 | *0.17* | 12.41 | *1.75* | 0.30 | *0.31* | 0.38 | *0.20* | 0.04 | *0.00* | 0.13 | *0.05* | 0.85 | *0.55* |
| FINE_7.4 | 3.76 | *0.09* | 2.19 | *0.31* | 10.79 | *0.52* | 0.17 | *0.11* | 0.21 | *0.13* | 0.04 | *0.01* | 0.11 | *0.06* | 0.53 | *0.30* |
| FINE_7.5 | 3.97 | *0.08* | 1.55 | *0.22* | 9.42 | *1.48* | 0.20 | *0.12* | 0.51 | *0.21* | 0.03 | *0.00* | 0.12 | *0.08* | 0.86 | *0.42* |
| **Spatial Grain** | **pH CaCl2** | | **Al cmolc/dm³** | | **H+AL cmolc/dm³** | | **Ca cmolc/dm³** | | **Mg cmolc/dm³** | | **Na cmolc/dm³** | | **K cmolc/dm³** | | **SB cmolc/dm³** | |

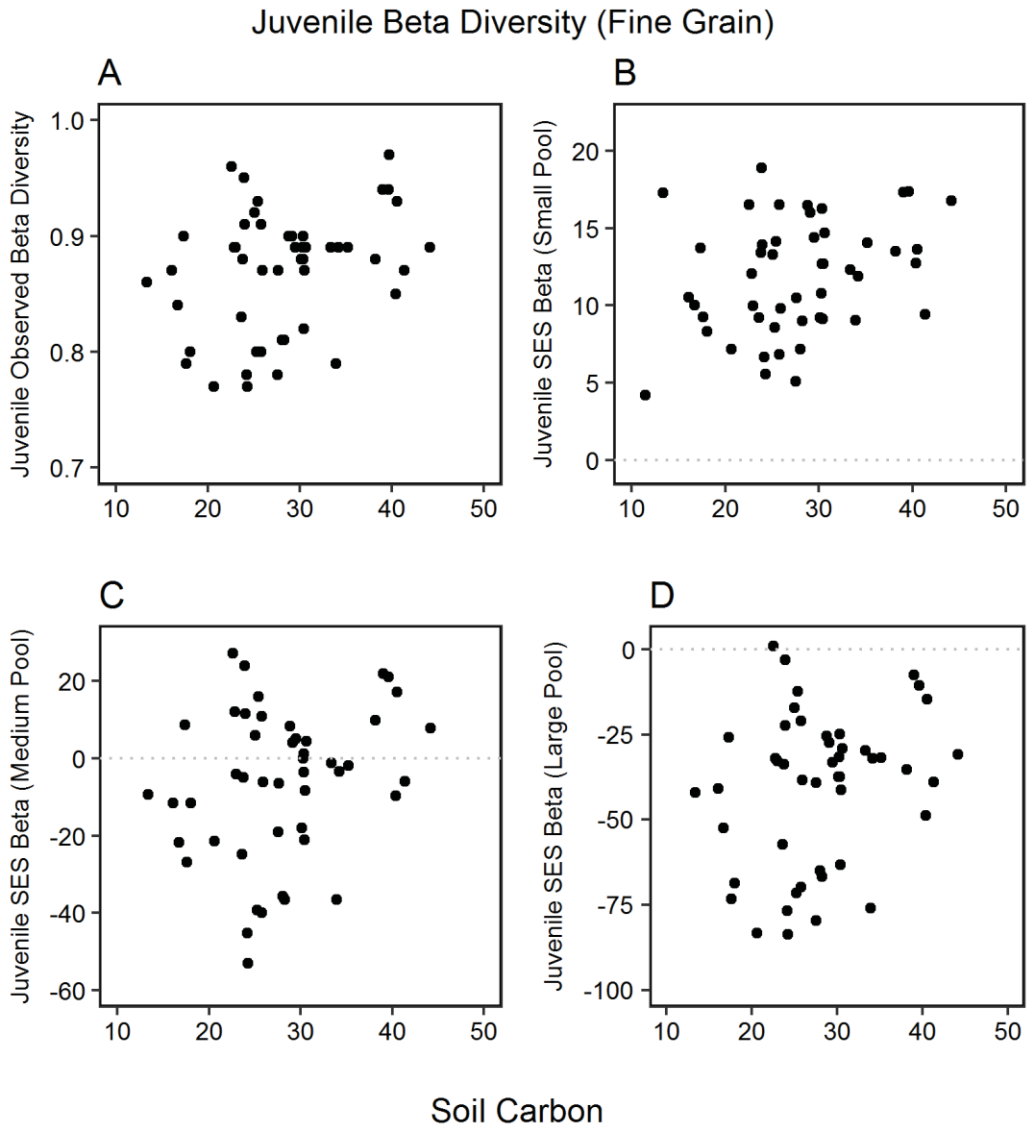
| | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| COARSE_8 | 3.74 | *0.12* | 3.03 | *0.54* | 13.71 | *1.79* | 0.30 | *0.12* | 0.37 | *0.22* | 0.05 | *0.02* | 0.13 | *0.04* | 0.85 | *0.35* |
| FINE_8.1 | 3.70 | *0.15* | 2.92 | *0.28* | 12.57 | *0.95* | 0.27 | *0.13* | 0.18 | *0.12* | 0.06 | *0.02* | 0.13 | *0.04* | 0.64 | *0.31* |
| FINE_8.2 | 3.91 | *0.05* | 2.41 | *0.32* | 12.13 | *0.70* | 0.40 | *0.21* | 0.54 | *0.28* | 0.04 | *0.02* | 0.13 | *0.05* | 1.11 | *0.54* |
| FINE_8.3 | 3.71 | *0.13* | 3.50 | *0.30* | 14.46 | *1.28* | 0.22 | *0.04* | 0.32 | *0.24* | 0.05 | *0.01* | 0.11 | *0.03* | 0.70 | *0.32* |
| FINE_8.4 | 3.70 | *0.11* | 3.07 | *0.58* | 14.62 | *2.89* | 0.34 | *0.07* | 0.25 | *0.18* | 0.04 | *0.02* | 0.12 | *0.04* | 0.75 | *0.30* |
| FINE_8.5 | 3.76 | *0.07* | 3.49 | *0.54* | 14.00 | *1.33* | 0.24 | *0.04* | 0.51 | *0.22* | 0.05 | *0.02* | 0.15 | *0.05* | 0.96 | *0.31* |
| COARSE_9 | 3.48 | *0.15* | 3.48 | *1.03* | 16.41 | *2.67* | 0.42 | *0.51* | 0.36 | *0.22* | 0.03 | *0.01* | 0.11 | *0.04* | 0.92 | *0.76* |
| FINE_9.1 | 3.38 | *0.15* | 4.39 | *1.08* | 18.01 | *2.01* | 0.28 | *0.41* | 0.32 | *0.26* | 0.03 | *0.02* | 0.10 | *0.04* | 0.73 | *0.73* |
| FINE_9.2 | 3.50 | *0.11* | 3.39 | *0.48* | 15.97 | *1.98* | 0.13 | *0.12* | 0.30 | *0.12* | 0.03 | *0.01* | 0.10 | *0.05* | 0.56 | *0.29* |
| FINE_9.3 | 3.41 | *0.15* | 3.88 | *1.36* | 19.74 | *2.06* | 0.94 | *0.98* | 0.56 | *0.32* | 0.05 | *0.01* | 0.13 | *0.04* | 1.68 | *1.34* |
| FINE_9.4 | 3.38 | *0.09* | 3.99 | *0.96* | 17.56 | *0.93* | 0.46 | *0.49* | 0.40 | *0.24* | 0.02 | *0.01* | 0.10 | *0.04* | 1.00 | *0.75* |
| FINE_9.5 | 3.67 | *0.09* | 2.52 | *0.67* | 13.90 | *0.73* | 0.50 | *0.39* | 0.35 | *0.21* | 0.03 | *0.00* | 0.14 | *0.07* | 1.02 | *0.67* |
| COARSE_10 | 3.81 | *0.13* | 2.74 | *0.54* | 13.33 | *1.83* | 0.26 | *0.16* | 0.35 | *0.19* | 0.04 | *0.02* | 0.13 | *0.04* | 0.78 | *0.35* |
| FINE_10.1 | 3.90 | *0.09* | 2.13 | *0.21* | 10.83 | *0.93* | 0.26 | *0.19* | 0.31 | *0.15* | 0.06 | *0.04* | 0.15 | *0.07* | 0.78 | *0.45* |
| FINE_10.2 | 3.96 | *0.05* | 2.44 | *0.19* | 13.32 | *1.19* | 0.25 | *0.19* | 0.52 | *0.22* | 0.04 | *0.01* | 0.15 | *0.06* | 0.96 | *0.47* |
| FINE_10.3 | 3.85 | *0.05* | 2.72 | *0.42* | 13.08 | *1.06* | 0.37 | *0.23* | 0.36 | *0.15* | 0.03 | *0.01* | 0.13 | *0.04* | 0.89 | *0.42* |
| FINE_10.4 | 3.70 | *0.14* | 3.55 | *0.57* | 15.73 | *1.94* | 0.12 | *0.10* | 0.29 | *0.17* | 0.04 | *0.02* | 0.12 | *0.05* | 0.58 | *0.33* |
| FINE_10.5 | 3.68 | *0.08* | 2.69 | *0.29* | 13.97 | *0.80* | 0.20 | *0.08* | 0.43 | *0.28* | 0.04 | *0.01* | 0.12 | *0.03* | 0.79 | *0.39* |

| Spatial Grain | P (mg/dm³) | | C (mg/dm³) | | V% | | m% | |
|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| COARSE_1 | 3.68 | *3.64* | 19.96 | *8.93* | 8.69 | *4.26* | 69.11 | *9.88* |
| FINE_1.1 | 3.26 | *1.22* | 30.43 | *2.73* | 9.12 | *3.96* | 72.77 | *10.95* |
| FINE_1.2 | 1.50 | *2.15* | 11.44 | *9.59* | 10.99 | *5.99* | 63.16 | *13.23* |
| FINE_1.3 | 10.14 | *3.57* | 23.99 | *8.56* | 7.32 | *1.72* | 73.60 | *5.84* |
| FINE_1.4 | 3.11 | *3.21* | 17.36 | *5.92* | 6.35 | *6.26* | 68.73 | *11.63* |
| FINE_1.5 | 1.93 | *1.48* | 17.61 | *6.87* | 10.52 | *5.75* | 65.00 | *14.18* |
| COARSE_2 | 5.61 | *3.85* | 37.26 | *12.01* | 4.09 | *0.95* | 83.56 | *2.94* |
| FINE_2.1 | 3.04 | *0.50* | 29.48 | *8.69* | 4.81 | *1.32* | 81.60 | *4.02* |
| FINE_2.2 | 7.93 | *5.24* | 44.16 | *11.27* | 3.36 | *1.07* | 85.82 | *3.78* |
| FINE_2.3 | 5.07 | *2.23* | 40.41 | *15.62* | 4.43 | *0.98* | 83.58 | *3.08* |
| FINE_2.4 | 4.92 | *3.52* | 33.95 | *3.98* | 3.69 | *0.80* | 82.87 | *2.26* |
| FINE_2.5 | 2.77 | *1.77* | 30.34 | *12.71* | 3.89 | *0.87* | 85.13 | *2.81* |
| COARSE_3 | 6.94 | *3.94* | 26.83 | *10.03* | 7.17 | *3.45* | 71.97 | *10.72* |
| FINE_3.1 | 8.08 | *4.63* | 27.57 | *11.50* | 6.24 | *3.41* | 76.85 | *10.27* |
| FINE_3.2 | 9.51 | *6.87* | 18.03 | *5.31* | 7.92 | *1.55* | 68.65 | *6.08* |
| FINE_3.3 | 4.28 | *2.29* | 20.64 | *8.45* | 8.14 | *1.10* | 68.95 | *3.85* |
| FINE_3.4 | 7.64 | *4.23* | 38.19 | *8.21* | 8.26 | *7.06* | 70.55 | *18.82* |
| FINE_3.5 | 4.80 | *2.60* | 22.83 | *9.14* | 7.86 | *2.20* | 68.82 | *12.74* |
| COARSE_4 | 3.66 | *2.48* | 26.12 | *10.54* | 6.99 | *3.92* | 73.20 | *13.22* |
| FINE_4.1 | 0.69 | *0.45* | 13.38 | *9.61* | 4.85 | *2.28* | 77.92 | *11.25* |
| FINE_4.2 | 4.55 | *2.57* | 30.64 | *13.97* | 6.39 | *3.16* | 72.52 | *12.43* |
| FINE_4.3 | 3.33 | *1.20* | 24.29 | *7.97* | 5.15 | *2.58* | 78.12 | *10.81* |
| FINE_4.4 | 2.66 | *1.91* | 28.81 | *10.26* | 5.12 | *2.60* | 81.04 | *8.66* |
| FINE_4.5 | 5.56 | *2.37* | 30.48 | *6.14* | 8.79 | *5.18* | 68.99 | *19.02* |
| COARSE_5 | 6.22 | *2.89* | 29.51 | *9.02* | 7.18 | *6.14* | 72.60 | *14.43* |
| FINE_5.1 | 6.43 | *3.46* | 25.79 | *10.66* | 2.94 | *1.85* | 81.25 | *9.19* |
| FINE_5.2 | 8.59 | *2.73* | 39.02 | *7.82* | 16.30 | *3.17* | 51.47 | *3.89* |
| FINE_5.3 | 6.94 | *2.09* | 24.18 | *6.49* | 3.87 | *1.57* | 87.53 | *5.40* |
| FINE_5.4 | 4.81 | *1.20* | 35.19 | *3.60* | 4.55 | *0.96* | 74.86 | *10.53* |
| FINE_5.5 | 5.49 | *2.95* | 28.26 | *10.53* | 4.88 | *2.62* | 72.61 | *10.24* |
| COARSE_6 | 4.23 | *1.27* | 22.50 | *7.95* | 7.34 | *4.31* | 73.72 | *13.23* |
| FINE_6.1 | 3.82 | *1.64* | 23.79 | *9.77* | 3.40 | *1.43* | 85.78 | *5.67* |
| FINE_6.2 | 5.39 | *1.46* | 23.00 | *9.42* | 9.93 | *5.87* | 66.50 | *16.25* |
| FINE_6.3 | 4.60 | *1.23* | 16.73 | *4.75* | 12.02 | *6.02* | 61.65 | *18.95* |
| FINE_6.4 | 4.09 | *0.63* | 25.29 | *7.12* | 7.58 | *2.86* | 68.92 | *12.01* |
| FINE_6.5 | 3.21 | *1.16* | 16.08 | *6.38* | 5.20 | *0.78* | 80.49 | *3.66* |
| COARSE_7 | 4.73 | *2.29* | 27.16 | *9.80* | 6.13 | *3.11* | 75.87 | *12.10* |
| FINE_7.1 | 5.21 | *3.48* | 33.34 | *12.31* | 5.26 | *1.29* | 81.05 | *2.78* |
| FINE_7.2 | 6.60 | *1.91* | 34.21 | *11.17* | 5.76 | *5.22* | 79.01 | *14.13* |
| FINE_7.3 | 3.53 | *2.04* | 28.05 | *9.15* | 6.10 | *2.87* | 77.09 | *12.06* |
| FINE_7.4 | 4.63 | *1.66* | 22.58 | *4.68* | 4.56 | *2.29* | 81.05 | *9.06* |

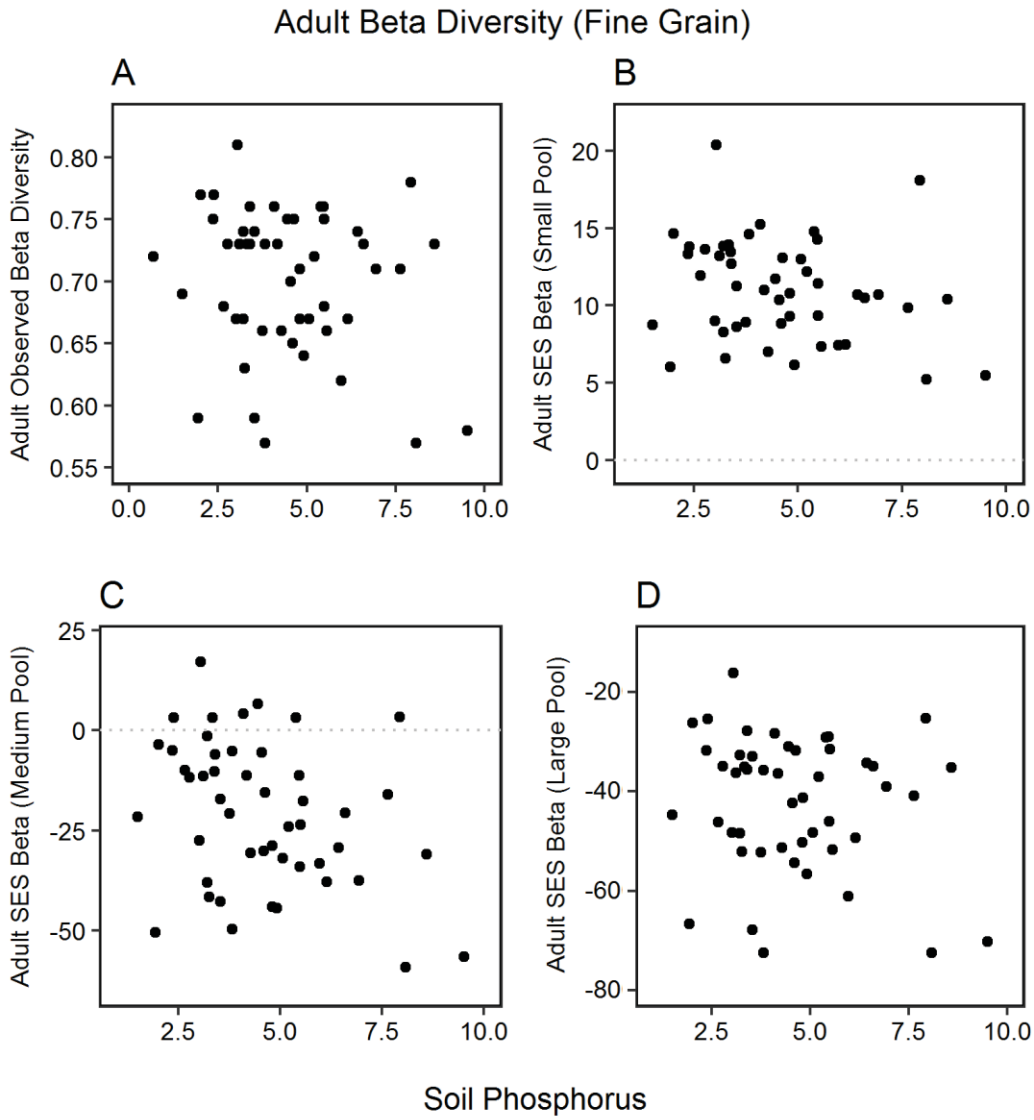
| Spatial Grain | P (mg/dm³) | | C (mg/dm³) | | V% | | m% | |
|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| FINE_7.5 | 5.47 | *2.87* | 23.92 | *11.22* | 8.15 | *2.74* | 65.13 | *13.45* |
| COARSE_8 | 4.44 | *2.39* | 32.29 | *12.83* | 5.80 | *2.34* | 78.21 | *8.54* |
| FINE_8.1 | 3.53 | *0.96* | 29.10 | *11.72* | 4.72 | *1.90* | 82.65 | *5.81* |
| FINE_8.2 | 5.97 | *2.29* | 23.63 | *13.88* | 8.26 | *3.72* | 69.14 | *12.99* |
| FINE_8.3 | 3.82 | *2.57* | 25.79 | *14.59* | 4.50 | *1.71* | 83.58 | *6.98* |
| FINE_8.4 | 3.75 | *2.80* | 40.55 | *15.02* | 4.79 | *1.01* | 80.64 | *4.59* |
| FINE_8.5 | 4.45 | *3.58* | 39.62 | *15.05* | 6.41 | *2.18* | 78.42 | *7.21* |
| COARSE_9 | 4.13 | *3.12* | 35.17 | *15.56* | 5.10 | *3.52* | 79.20 | *15.11* |
| FINE_9.1 | 2.01 | *0.80* | 25.05 | *13.98* | 3.95 | *4.06* | 85.12 | *15.80* |
| FINE_9.2 | 5.48 | *3.88* | 30.16 | *6.39* | 3.28 | *1.37* | 85.92 | *7.33* |
| FINE_9.3 | 6.15 | *5.05* | 50.19 | *23.94* | 7.46 | *5.18* | 69.87 | *24.15* |
| FINE_9.4 | 3.21 | *1.33* | 39.73 | *11.69* | 5.39 | *4.12* | 79.57 | *16.17* |
| FINE_9.5 | 3.40 | *1.94* | 30.34 | *16.13* | 6.74 | *4.35* | 71.54 | *18.56* |
| COARSE_10 | 2.89 | *1.63* | 29.39 | *10.69* | 5.49 | *2.24* | 78.03 | *8.77* |
| FINE_10.1 | 4.18 | *1.85* | 25.43 | *6.24* | 6.50 | *3.01* | 74.27 | *10.99* |
| FINE_10.2 | 2.39 | *2.22* | 41.37 | *11.76* | 6.60 | *2.71* | 72.55 | *9.94* |
| FINE_10.3 | 3.39 | *1.80* | 25.94 | *7.47* | 6.24 | *2.55* | 75.55 | *11.15* |
| FINE_10.4 | 2.36 | *1.73* | 27.60 | *15.96* | 3.41 | *1.52* | 86.68 | *5.02* |
| FINE_10.5 | 3.01 | *1.28* | 30.28 | *11.01* | 5.22 | *2.23* | 78.04 | *8.17* |



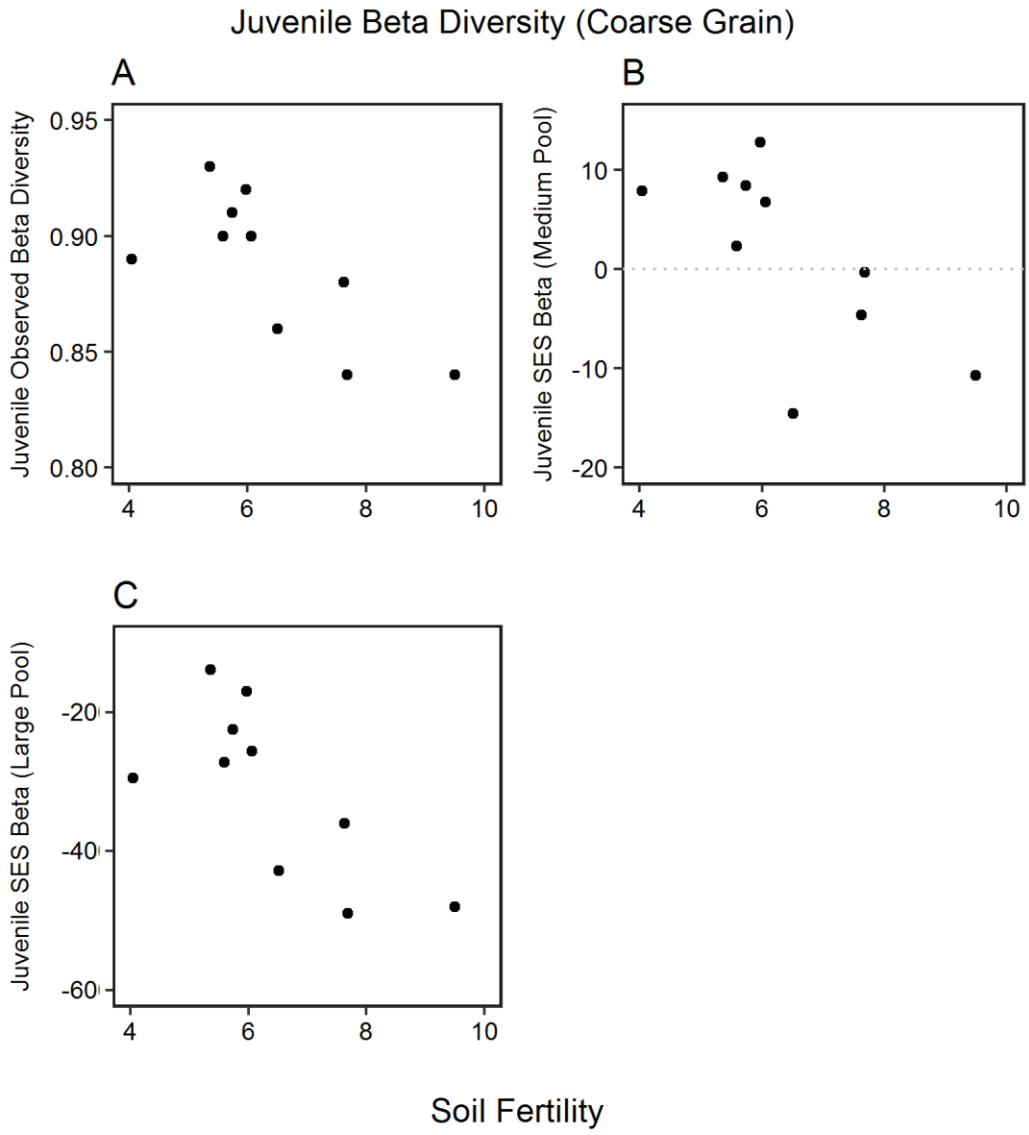

**Appendix B1** – Principal Component Analysis (PCA) of 12 soil chemical variables of the Guaricica Natural Reserve. A) Plot of axes 1 (40 %) and 2 (23 %); B) Plot of axes 1 e 3 (14%). In Chapter 1, we used only uncorrelated biological importance variables belonging to each of the three axes, selected by the Broken-Stick criterion, to test the relationship with the beta diversity of trees: Axes 1) Carbon (C); Axes 2) Base saturation (V); Axes 3) Phosphorus (P). In Chapter 3, the three axes were used as predictor variables to test the response of functional structure metrics (CWM and Rao) to the variation in sample effort.



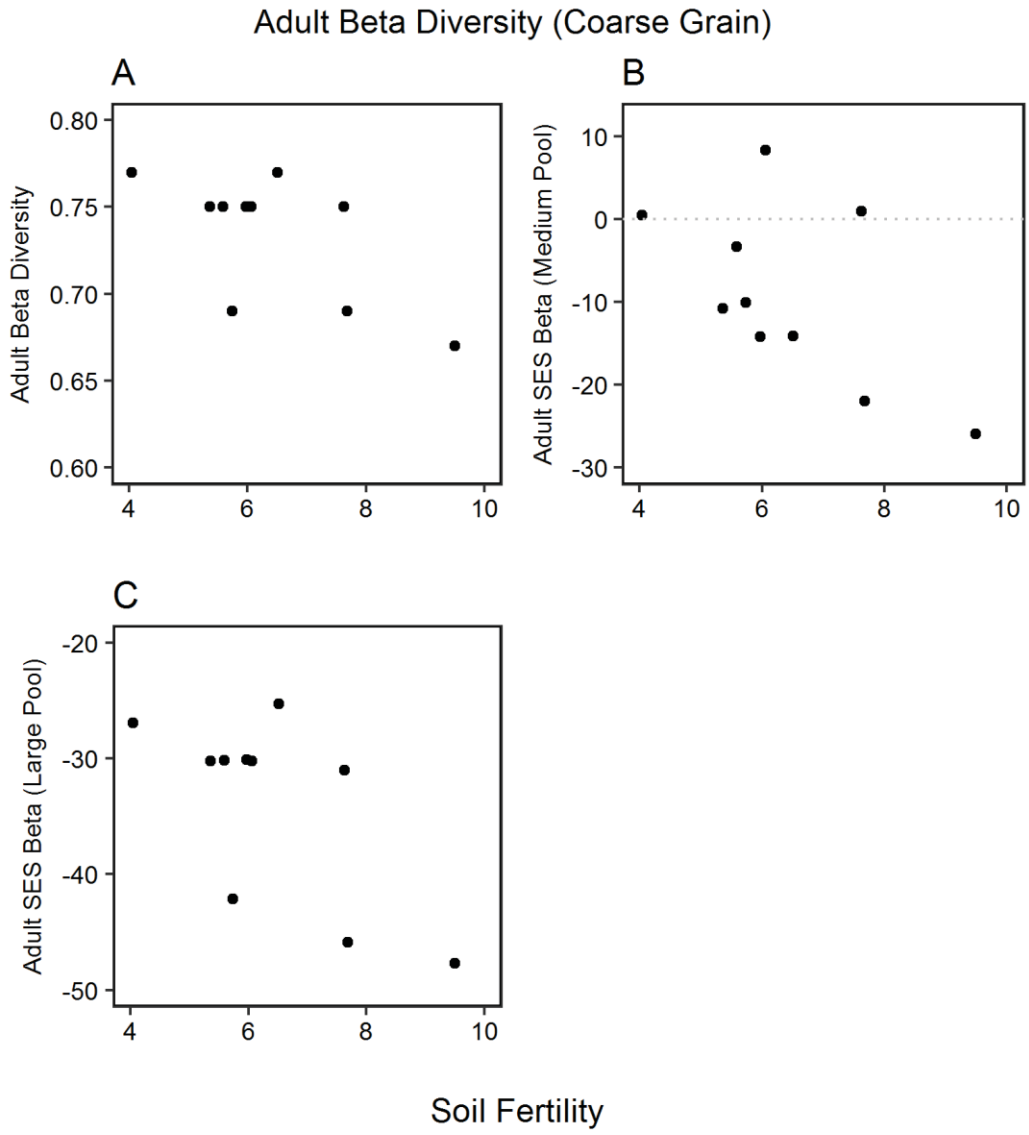

**Appendix C1** - Dispersion diagram showing the relationship between juvenile beta diversity and soil carbon in the fine grain.




**Appendix D1** - Dispersion diagram showing the relationship between adult beta diversity and soil phosphorus in the fine grain.




**Appendix E1** - Dispersion diagram showing the relationship between juvenile beta diversity and soil fertility in the coarse grain.




**Appendix F1** - Dispersion diagram showing the relationship between adult beta diversity and soil fertility in the coarse grain.

# CAPÍTULO 2

## Environmental filtering determines species richness in a mega-diverse tropical forest


### Abstract

Among the niche processes evoked to explain species richness patterns in communities are limiting similarity and environmental filtering. Limiting similarity results in the exclusion of subordinate species by superior competitors and reduce species richness, while environmental filtering restrict niche dimensions and also limits species richness. Analyzing changes in mean and variance of functional traits along gradients is the most common way of testing the action of these niche mechanisms. However, a possible limitation of this approach is that it does not allow us to infer how patterns of occupation of niche space contribute to species richness gradients. As species richness increases, habitat filtering should constrain the expansion of functional volume and increase niche packing, while resource partitioning should restrict the degree of niche overlap between species in the functional volume and decrease niche packing. In this study, we combine the two approaches to analyze processes that explain species richness in a mega-diverse tropical forest. Specifically, we answer the following questions: 1) What is the relationship between changes in mean and variance of traits that inform about the competitive ability (maximum height and SLA), and species richness? 2) What is the relationship between functional volume occupation and species richness? 3) How much are species packaged within the functional volume? We analyzed these questions in relation to three spatial scales, defined from three different species pool sizes. We found no evidence that competition or resource partitioning drives the species richness gradient. As species are added to a few plots, they are packaged within the functional volume which is lower than expected. We found that this pattern is related to the larger species pool and that on smaller scales no niche process prevailed. We conclude that environmental filtering is the main process generating richness in this plots.

Keywords: Functional richness. CWM. Niche space. Niche packing. Limiting similarity.

## 1. Introduction

Understanding the processes that determine plant diversity in tropical forests has been a challenge for ecologists for several decades (KRAFT *et al.*, 2008). Studies suggest that patterns of diversity are influenced by assembly processes that differ in relative importance. Neutral theory suggests that community assembly is determined by demographic stochasticity and dispersal limitation, i.e. independently of species functional traits (HUBBEL, 2001). However, the idea that functional differences and the strength of species interactions determine the total niche space available within a local community and that this limits the pattern of species distribution, abundance and richness has been constantly corroborated (DÍAZ & CABIDO, 2001, CHASE & LEIBOLD 2003). This idea is based on the theories of Hutchinson's n-dimensional niche (HUTCHINSON, 1957), the limiting similarity (MACARTHUR & LEVINS, 1967) and environmental filtering (KEDDY, 1992). Environmental filtering is known to restrict the niche in a few dimensions and lead to overlapping of species in the functional space (KEDDY, 1992). Limiting similarity refer to biotic interactions (e.g., interespecific competition) that reduces the likelihood of co-occurrence of similar species through competitive exclusion (MACARTHUR & LEVINS, 1967).

Analyses of trait mean and variance shifts along gradients have been the most common way of investigating the action of this niche processes (environmental filtering and competitive exclusion) in plant communities (CORNWELL & ACKERLY, 2009). For example, changes in trait means and variance linked to the competitive ability of plants, along richness gradients, could inform if competitive exclusion is an driver of these gradients (SCHAMP & AARSSEN, 2009): for plant species, maximum height is an important predictor of light ability competitive, since tall plants can obtain this resource more easily at the expense of lower plants that can be excluded by competition. Thus, the decrease in the maximum height in plots of higher richness would be evidence

that the absence of strong competitors favors the richness by allowing the persistence of subordinate species. The same relationship can be expected for the specific leaf area (SLA), which is a functional trait related to efficiency in using resources; thus, higher SLA averages reflect a greater competitive ability. Already the greater variance than expected of these traits in plots of higher richness can reinforce the role of the competition.

A possible limitation for this approach is that it does not allow us to say how patterns of occupation of niche space contribute to the species richness gradients. One way to measure the niche space is to calculate the functional volume, defined as the total volume of the functional space filled by the species (VILLÉGER *et al*., 1998). As species richness increases, habitat filtering should constrain the expansion of total functional volume, which should be less than expected at random. On the other hand, the biotic interactions tend to expand the functional volume to the extent that the competitive exclusion of subordinate species is replaced by coexistence mechanisms, such as resource partitioning. Resource partitioning, can explain the expansion of total functional volume because, as new species are added to the community, they come to occupy most extreme portions of the functional space before unoccupied, avoiding niche overlap and favoring species richness. In such approach, positive relationship between functional volume and species richness, and a functional volume larger than expected under null expectation means that species are less overlapped, indicating low competition and greater likelihood of resource partitioning.

Often, the species are packing into the functional volume; thus, as new species are added to the community, they can be accommodated in pre-existing spaces of the functional volume so as to specialize in small intermediate portions (RICKLEFS & TRAVIS, 1980). In this sense, niche packing allows more species to be hermetically arranged within functional volume without necessarily expanding (RICKLEFS & COX, 1977). One way of quantifying niche packing is by measuring the functional distance between species in the niche space (SWENSON & WEISER, 2014). Thus, a negative relationship between niche packing and species richness indicates that species are packaged within the functional volume; species can be packaged through environmental filtering or specialization in the niche space (resource partitioning). Quantifying the

degree of species spacing within the functional volume and how much it differs from the null expectation is crucial to distinguish between one and another process; greater than expected functional distance reflects resource partitioning, whereas smaller than expected functional distance reflects environmental filtering.

For plant species, the action of different niche processes has been explored with the use of key functional traits. For example, Westoby (1998) established the *LHS* scheme (specific leaf area-*SLA*, maximum height and seed mass), which represents axes of functionally independent orthogonal traits, that describe major ecological strategies of plants. Lower SLA (due to thicker and/or more dense leaves) contributes to long leaf survival, nutrient retention, and protection from desiccation. Higher SLA values indicate use resource efficiency and rapid growth, which can be considered a competitive advantage (WRIGHT *et al*., 2004); this is a trait that reflected both competitive ability (higher SLA) and efficiency in resource use (lower SLA). Seed mass (SM) values represent a trade-off between the production of few large seeds *versus* many small seeds, which influences seed dispersal and seedling survival and is associated with efficiency in resource capture and use (WESTOBY *et al.* 1992, MOLES & WESTOBY, 2006). Finally, maximum height (MH) is related to light competition and may reflect plant competitive ability; as tall plants shade lows but the opposite does not occur, maximum height is seen as an important trait that describes competitive ability of plants, in which taller species are considered more successful competitors compared to shorter ones (FALSTER & WESTOBY, 2003). Combined, these traits and the different methods mentioned above can contribute to elucidated key determinants of species richness at different scales in communities.

Recent studies developed at broad scales (regional and global) reported a positive relationship between functional volume and plant species richness, but when compared to null expectation, functional volume is lower than expected indicating the effect of environmental filtering (LAMANNA *et al.*, 2014, SWENSON & WEISER, 2014, LI *et al.*, 2017). Among the few studies analyzing the relationship between niche packing in functional volume and plant species richness, Swenson & Weiser (2014) found that niche packing is larger as species richness increased, but the species overlapped less than the expected

in the functional volume indicating limiting similarity. Conversely, Li *et al.* (2017), including intraspecific variation, observed that niche packing makes species more similar within the functional space in response to environmental filtering. Although these studies advanced our understanding on the relation between species richness, functional volume and niche packing, we still lack the information whether niche space occupation patterns observed for regional and global scales apply to local scales of neighborhood, especially in systems that accommodate a great amount of species. In this study, we tested the hypothesis that niche mechanisms - competitive exclusion, resource partitioning and environmental filtering – affect the species richness gradient, on a neighborhood local scale, in a mega-diverse tropical forest in southern Brazil. Specifically, we investigated how the means and variance of traits linked to the plant competitive ability (MH and SLA), as well as the occupation and packing of the niche volume (calculated for traits related to resource capture, SM and SLA) change along the species richness gradient. We aimed to answer the following questions:

1) What is the relationship between changes in mean and variance of traits that inform about the competitive ability (maximum height and SLA), and species richness?

If the absence of superior competitors is determinant for the permanence of subordinates, thus favoring the species richness, the mean and variance of traits related to the competitive ability (MH and SLA), must be higher than expected, but mean will be negatively and variance will be positively correlated to species richness.

2) What is the relationship between functional volume occupation and species richness?

If resource partitioning influences the species richness gradient, we expect the functional volume to be larger than expected and positively correlated to species richness; if environmental filtering influences the species richness gradient, the functional volume should be smaller than expected, and the relationship with richness will be positive, since in species rich plots the functional volume should be less restricted even with the effect of environmental filtering.

3) How much are species packaged within the functional volume?

If resource partitioning influences the species richness gradient, the niche packing should be negatively related to species richness and higher than expected at random, indicating that the species are more specialized in the functional volume; if the environmental filtering influences the species richness gradient, the niche packing should be negatively related to species richness and lower than expected at random, indicating that the species are overlaid on the functional space.

It is known that different niche processes can act simultaneously in local communities and that the relative strength of each is captured through spatial scales. Thus, smaller spatial scales capture biotic interactions more efficiently, while larger scales capture the effects of environmental filtering in the community. Considering this, we analyzed how the relationship between niche mechanisms and species richness gradient changes with different species pool sizes (small, medium and large), and we did the following predictions (fig. 1).

1) Small pool size - At this scale, the effects of biotic interactions on the richness will be more evident. Thus, we expected: 1) mean and variance of traits related to competitive ability (MH and SLA) will be higher than expected, but means will be negatively correlated to species richness (fig 1A), and variance will be positively correlated to species richness (fig 1B), indicating competitive exclusion; 2) the functional volume will be higher than expected at random and positively correlated with species richness, indicating resource partitioning (fig 1C); 3) the niche packing will be higher than expected at random and negatively correlated with species richness, indicating resource partitioning (fig 1D).
2) Medium pool size - Both biotic interactions and environmental filtering may occur because this scale represents a transition between the small and large pool sizes. With the two processes acting simultaneously, random patterns will be generated. Thus, we expect to find no significant relationship between the species richness gradient and: 1) shifts in means and variance of traits related to the competitive ability (MH and SLA) (fig 1E-F); 2) functional volume (fig 1G); 3) niche packing (fig 1H).
3) Large pool size - At this scale, large-scale environmental variations will be more visible because increasing spatial scales incorporate more

environmental heterogeneity. Thus, we expected: 1) decrease the effect of competition in richness, so mean and the variance of traits related to the competitive ability (MH and SLA) will be smaller than expected given the environmental filtering, and positively correlated with the species richness (fig 1I-J), since plant growth decreasing can be limited under this conditions and the decline of SLA can mean strategy of investing in resources in extreme environments; 2) functional volume will be smaller than expected and positively correlated to species richness, indicating environmental filtering (fig 1K); 3) the niche packing will be lower than expected and negatively correlated to species richness (fig 1L), indicating environmental filtering.

## 2. Material and Method

### *2.1 Study area*

We carried out the study at the Guaricica Natural Reserve (25º19'15"S and 45º42'24"W), located in the municipality of Antonina, Paraná Sate, southern Brazil. The Reserve has 8,600 ha and is included in the Guaraqueçaba Environmental Protection Area, one of the largest protected and continuous remnant areas of the Brazilian Atlantic Forest (FERRETTI & BRITEZ, 2006). The climate is subtropical humid mesothermal. The mean temperature is 21°C in the warmer months and 18°C in the colder months, with annual rainfall around 2,000 to 3,000 mm and relative air humidity around 85% (MAACK, 2012). The vegetation in the region is dominated by submontane and lowland dense ombrophilous forests (IBGE, 2012). Forests are marked by three well defined strata, canopies of 20-30 m in height, and tree species richness of more than 300 species (BORGO *et al.*, 2011).

### *2.2 Species data*

A RAPELD module was established in a region of Submontane Rainforest in the reserve. This is a modification of the 0.1-ha plot method developed by Alwyn Gentry and adapted to long-term ecological research sites that allow rapid inventories (MAGNUSSON *et al.*, 2005). The RAPELD module consists of a set of ten 1-ha plots, systematically distributed in two rows with

five plots, spaced 1 km from each other. Each plot had 250 m long by 40 m wide and its center followed the ground level curve, minimizing internal variations in topography and soil. Altitude between plots ranged from 20 to 470 m a.s.l, while slope inclination ranged from 6° to 22°.

Vegetation survey was done for three different plant sizes, using varying sampling ranges (fig. 2a): Sampling range 1 - Ranges 1.5-m wide , concentric with the 1-ha plot were used for sampling individuals with a diameter at breast height (DBH, 1.3 m) ≥ 1 cm; Sampling range 2 - Ranges 20-m wide, also concentric with the 1-ha plot, were used for sampling individuals with DBH ≥ 5 cm; Sampling range 3 – Ranges 40-m wide, representing the whole plot area, were used for sampling individuals with DBH ≥ 10 cm. The trees in the three ranges were measured, collected and identified at the species level.

For subsequent analyses, we subdivided each 1 ha-plot into 10 x 10 m subplots, thus, each 1 ha-plot generated hundred subplots totaling thousand (100 subplots x 10 plots) (fig 2b). We believe that this size is large enough to represent the forest community and small enough to reduce the influence of habitat heterogeneity and capture biotic interactions. For analytical reasons, only subplots that had at least five species and species that had at least five individuals per subplot were kept for subsequent analyzes. Thus, the total subplots used were reduced from 1000 to 721.

*2.3 Functional traits*

We chose three functional traits that describe the main axes of ecological strategies for plants (WESTOBY, 1998): specific leaf area (SLA), maximum height (MH) and seed mass (SM).

SLA: As other leaf traits, SLA to play a particularly important role in carbon assimilation, water relations and energy balance. Is negatively correlated with leaf life span and assimilation rates. Values of *SLA* represent a trade-off between slow growth and high leaf longevity (lower *SLA*) *versus* rapid growth and better competitive ability (higher *SLA*) (WRIGHT *et al.*, 2004). In this study SLA was used as trait related to both competitive ability and resource capture.

For SLA measurement, we collected five fully expanded leaves, exposed to sun and without herbivory, for five individuals of each species (adults, only) with DBH ≥ 5 cm (ranges 2 and 3), which summed 80% of the relative abundance in each 1 ha-plot. The newly collected leaves were scanned and the scanned images were used to measure the leaf area in the *ImageJ* software (RASBAND, 2012). After, they were oven dried for 72 hours and weighed. To obtain the SLA ($cm^2$) we divided the area by the dry weight of leaves and calculated the mean for each species. Thus, SLA for each species had a representation of at least five and at most fifty individuals (five individuals multiplied by ten 1 ha-plots).

Maximum Height: The maximum height is one of the main traits related to light capture and plants competitive ability, due to the advantages that tall plants have over small ones.

Tree height (m) was obtained with electronic tape for all individuals of all species; when not possible the height was estimated by visual comparison. The maximum height (MH) observed in the study area for each species was used as trait.

Seed mass: is important for regeneration, the competition–colonization trade-off (COOMES & GRUBB, 2003), and tied to plant stature (MOLES & WESTOBY, 2006). Here, we consider seed mass as an important trait related to the capture and use of resources.

Seed mass (mg) was obtained from several sources in the literature. We limited its collection to studies developed in the Atlantic Rainforest and expanded to other formations only when the data were nonexistent in the first (Appendix A2). When different values were found for the same species, we calculated the mean; in the absence of data for a species, we used the mean for the genus.

### *2.4 Statistical analysis*

To analyze the relationship between species richness (*S*), defined as the total species in each 10 x 10 m-subplot, with competitive exclusion, niche volume and niche packing, we first quantified the observed values in each subplot for each metric as described below:

*CWM* - we calculated observed trait community-weighted mean (*CWM*) related to plant competitive ability (MH and SLA) for each 10 x 10 m-subplots. We also calculated the observed community-weighted variance (*CWV*) of these traits, which may inform if, within subplots with higher MH and SLA, the variance is large enough to reflect interspecific competition. If the variance is greater than expected and positively correlated to richness, then we infer that competition prevails.

*Functional volume* - we quantified the functional volume observed for each 10 x 10 m-subplot using the index of functional richness (*FRic*; CORNWELL *et al.*, 2006; VILLÉGER *et al.*, 2008) considering only the traits related to obtaining and use resources (SLA and SM). Using the "convex hull" algorithm, the most extreme points of trait values in the two-dimensional trait space were determined; then the points were connected to construct the convex hull and, finally, the internal volume was calculated (CORNWELL *et al.*, 2006; VILLÉGER *et al.*, 2008).

*Niche packing* - we quantified the observed niche packing using the mean nearest neighbor distance (*MNND*) in each 10 x 10 m-subplot (SWENSON & WEISER, 2014). This index uses an Euclidean distance matrix between species considering differences in traits (SLA and SM), thereby informing how close the species are arranged within the bivariate functional space. The observed value of *MNND* is compared to a null expectation. *MNND* values may be larger or smaller than expected, possibly indicating niche differentiation or overlap, respectively. Richness gradients driven by niche packing tend to be negatively correlated to *MNND* (SWENSON & WEISER, 2014).

In order to calculate expected values of *CWM*, *CWV*, *FRic* and *MNND*, we used a null model that shuffles species names in the trait matrix and recalculates each metric 999 times while maintaining species richness. By doing so we generated 999 expected values for each metric, from which we obtained a mean value of the metric. Species names were shuffled from three different species pool sizes defined on the basis of total tree species potentially able to disperse across space within a given scale as follows.

*Small species pool* - Each 1 ha-plot was subdivided into five segments of 200 $m^2$; each segment containing twenty 10 x 10 m-subplots. The observed

metric values for each of these subplots were compared to the null expectation according to a species pool composed of all the species recorded in the 200-$m^2$ segment to which the subplot belonged (fig 2D).

*Medium species pool* - Each 1-ha plot contains a maximum of hundred 10 x 10 m subplots; for each of these subplots, the species pool was composed of all the species in the 1 ha-plot to which the subplot belonged (fig 2c).

*Large species pool*: This pool includes all 10 x 10 m-subplots of ten 1 ha-plots. Thus, for each 10 x 10 m-subplot, the species pool was composed of all the species sampled in the 721 subplots (10 ha module) (fig. 2b).

Then, to verify if the observed *CWM*, *CWV*, *FRic* and *MNND* values differed significantly from the null expectation in each subplot, we calculated the standardized effect size (*SES*) for each metric as:

$$SES = \frac{\left(Metric_{observed} - Metric_{expected}\right)}{Standard\ Deviation_{expected}}$$

Significantly positive or negative *SES* indicate that the observed value of the metric is higher or lower than expected at random from a given species pool size, respectively. Non-significant (i.e. null) SES indicate that the metric does not differ from the expected at random from the pool. The SES represents a correction for the sampling effect, which can generate skewed non-random patterns.We considered *p-values* below 0.025 and above 0.975 (lower and higher than expected, respectively) as significant.

Finally, as the data did not present a normal distribution (analyzed by the Shapiro-Wilk test), we used Spearman correlation to analyze the relationship between species richness and *CWM*, *CWV*, *FRic* and *MNND*. All analyzes were conducted in software *R v.3.4.0* (R CORE DEVELOPMENT TEAM, 2017).

## 3. Results

We measured functional traits for 146 species of adult plants. The mean of species per subplot (10 x 10 m) was nine. The plots with the lowest richness presented, in average, five species, and the plots with the highest richness, twenty-five.

*3.1. Community Weight-Mean (CWM) and Community Weight-Variance (CWV)*

The observed $CWM_{MH}$ was negatively correlated to *S* (*rs* = -0.23, *p* = < 0.0001, fig 3A), presenting a wedge pattern with a convergence of values at the high end of the species richness gradient. The $CWM_{MH}$ was larger than expected from the null model in 14.8% of subplots compared to the large pool, 7.6% compared to the medium pool and 2.96% compared to the small pool. The *SES* $CWM_{MH}$ was negatively correlated to *S* in the large (*rs* = -0.10, *p* = 0.02, fig 3B) and medium pools (*rs* = -0.20, *p* = <0.001, fig 3C) but not correlated in the small pool (rs = 0.05, p = 0.34, fig 3D). The $CWV_{MH}$ was positively correlated with *S* (*rs* = 0.35, *p* = <0.001, fig 4A), but *SES* $CWV_{MH}$ was not correlated with *S* in any of the three pool sizes (fig 4B-D).

The observed $CWM_{SLA}$ was not correlated with *S* (*rs* = 0.06, *p* = 0.07, fig 5A). The $SES_{SLA}$ was generally larger than expected, and approximately 11% of the subplots differed from that expected in the large pool, 13% in the medium pool and 12% in the small pool. The $SES_{SLA}$ was slightly positively correlated to *S* in relation to large pool (*rs* = 0.10, *p* = 0.005, fig 5B), but not correlated in relation to medium and small pools (fig 5C and 5D). The observed $CWV_{SLA}$ was positively correlated to *S* (*rs* = 0.23, *p* = <0.001, fig 6A), but *SES* $CWV_{SLA}$ was not correlated to *S* in relation to any of the three pool sizes (fig 6 B-D).

*3.2. Functional Volume (FRic)*

The observed functional volume (*FRic*) was positively correlated with *S* (*rs* = 0.48, *p* = < 2.2e-16, fig 7A). The *SES FRic* was lower than expected at random for 8% of the subplots compared to the large pool (only 2% were higher than expected), for 4% compared to the medium pool (only 1% were higher than expected), and for less than 1% compared to the small pool (1.84% were higher than expected). The correlation between *SES FRic* and *S* was negative on the large pool (*rs* = -0.34, *p* <0.001, fig 7B), slightly negative on the medium pool (*rs* = -0.14, *p* < 0.001, fig 7C) and not significant on the small pool (*rs* = 0.08, *p* = 0.14, fig 7D).

*3.3. Niche packing (MNND)*

Observed niche packing (*MNND*) was negatively correlated to *S* (*rs* = -0.15, *p* = <0.001, fig 8A). The *SES MNND* presented negative significant values regardless of the pool size analyzed, indicating that species are closer in the functional space than expected under a null model. The *MNND* was smaller than expected in approximately 5% of the subplots compared to the large pool, 3% compared to the medium pool and 2% compared to the small pool. The *MNND* was larger than expected in less than 1% of the subplots compared to the large pool, 1.4% compared to the medium pool, and 0.7% compared to the small pool. The relationship between *SES MNND* and *S* was significantly negative compared to the large (*rs* = -0.22, *p* = <0.001, fig.8B) and medium pools (*rs* = -0.12, *p* = 0.001, fig 8C), but not the small pool (*rs* = -0.06, *p* = 0.15, fig 8D).

## 4. Discussion

We began investigating the influence of competition on the species richness gradient through the analysis of the relationship between richness and traits linked to the competitive ability of plants. We found no evidence of competition with respect to SLA, but this may be due to the fact that SLA responds well to both interactions and the environment (Westoby, 1998). We observed that species richness increases as the presence of more successful competitors (taller trees) decreases, and co-occurring species in several subplots are higher than expected at random, which, at first sight, could be an indication that competition predominates in most of these subplots. However, despite the general relationship between $CWM_{MH}$ and *S* being negative, in the subplots where the maximum height was significantly higher than expected, we did not observe diminution of height with *S* increase, as hypothesized. Moreover, a wedge pattern was found in the general relationship between $CWM_{MH}$ and *S*, indicating that, in the most rich subplots, the $CWM_{MH}$ is not smaller, but intermediate in relation to all subplots. Finally, we verified that the observed $CWV_{MH}$ was higher in more rich subplots, but, when removing the

sampling effect, the maximum height varied in the same way along the *S* gradient. Despite this, several plots showed higher maximum height than expected (both mean and variance), which may be an indication that competition should occur in some of them, although it does not influence the species richness gradient. This indicates that, regardless of the species number in the subplots or the pool size analyzed, the MH does not explain the biotic interactions in high richness. Although light competition is important in structuring forest communities and height is a determinant of plants competitive ability, the absence of higher competitors in subplots of greater species richness can be explained by the absence of adequate habitats for higher species, which require specific habitats, or by the predominance of smaller habitat patches, which will therefore serve more adequately to smaller or intermediate plants (AARSSEN *et al.*, 2006). Thus, we conclude that the general observed pattern in relation to $CWM_{MH}$ can be result of environmental filtering and not competitive exclusion.

The observed functional volume expands as species are added to subplots, in other words, subplots that hold more species are those where niche space occupancy is made more spaced. However, compared to the null model, the functional volume in a minority of subplots was significantly different from expected and we observed two interesting results: first, as *S* increases from one subplot to the next in the medium and large pools, the functional volume decreases indicating that the subplots of greater richness are actually less diverse and that the relationship between the functional volume observed and *S* reflects possibly a sampling effect. Second, in the subplots that differed from the expected, the functional volume was generally smaller than expected at random, regardless of the pool size, and only on the large pool, the functional volume was even lower as the species richness increased, indicating that functional volume is much more restricted in subplots that accommodate more species on large scales. The negative relationship between functional volume and species richness does not reflect our expectation regarding environmental filtering, but this does not mean that this process is not working; it is expected that the functional volume will be restricted by environmental filtering but interactions between species will determine its expansion. As in most plots the functional volume was smaller than expected we believe that environmental

filtering predominates, but species do not interact enough to expand it where the richness is greater. This probably represents further evidence that species are more functionally similar because they are filtered into richer plots. Thus, these results combine with the environmental filtering hypothesis (KEDDY, 1992), as well as that observed by other authors (LAMANNA *et al.*, 2014; SWENSON & WEISER, 2014; LI *et al.*, 2017) and predicted to occur on the large pool of our study.

The way the species dispose within the functional volume can favor coexistence even when it is restricted by the environmental filtering, as discussed above. To confirm whether species do not actually interact within the restricted functional volume by environmental filtering, we look at niche packing. Although only analysis that include intraspecific variation can say with certainty the degree of species overlap/spacing within the functional volume (VIOLLE *et al.*, 2012; LAMANNA *et al.*, 2014; LI *et al.*, 2017), we observed that, with the increase of *S*, the degree of niche packing increases (equivalent to the decrease in functional distance as measured by the *MNND*), and although few subplots differed from those expected, *MNND* was smaller than expected and became even smaller with S increasing on the large pool. This means that in richer subplots, on this pool size, species are functionally more similar in relation to resource capture and use traits. This observation shows that the *S* increases because species are hermetically overlapping within the functional space, and not specialized, while reinforcing the role of the abiotic filters. Our results are somewhat different from Swenson and Weiser (2014), who found that functional volume was restricted by environmental filtering in North America, but within the restricted volume, the species competed with each other. Our results were similar to Li et al. (2017), who included intraspecific variation in their analysis and found that environmental filtering determines niche occupation and niche packing of plant assemblages at global scale. Animal assemblages have been better documented, and the results demonstrate that increased niche packing is the main determinant of bird species richness at regional (PIGOT *et al.*, 2016) and global scales (PELLISSIER *et al.*, 2018).

The reason that we have not found clear evidence of any niche process acting on the small pool sizes is possibly attributed to the absence of major

environmental heterogeneity at these scales, which has been increasingly important in facilitating the coexistence of an undefined number of species (FANG *et al.*, 2016). It was only when we expanded the pool size and included possible environmental variations that niche processes, in this case, environmental filtering, raised. Although biotic interactions are theoretically expected to occur at smaller scales, for large trees, such as measures in our system, if the scale is too small it will hide and the action of these processes rather than helping to identify them. Thus, we believe that when we consider the large pool (10 ha), we reach the minimum viable spatial scale for the capture of neighborhood-scale niche processes in our study system.

For most plots, we found that CWM, CWV, FRic, and MNND were not different from null expectation, a result expected to occur mainly in the medium pool. This pattern is much more complex to understand, since may come from different sources, including opposite niche mechanisms acting simultaneously or stochastic process. Thus, we do not rule out the possibility that niche processes, including biotic interactions, operate in most of the subplots and that we did not have the ability to capture them from our statistical artifacts, though we were able to detect environmental filtering in some subplots of our study system. Biotic interactions can happen on even finer, not necessarily spatial, scales, and can involve different groups of functional traits not considered here. Thus, the use of sufficiently potent statistical artifacts to capture this process is fundamental, as traits representing large portions of n-dimensional niche space and the inclusion of intraspecific variation.

## 5. Conclusions

We found that competition must occur in some plots, but does not influence the species richness gradient. However, we found that as species are added to the community, in relation to large pool size, are hermetically overlaid in the functional space, restricted by environmental filtering, so that environmental filtering is a scale - dependent process responsible for generating and maintaining the species richness on a neighborhood scale. Our results provide a basis for understanding the processes that drive species richness in highly diverse tropical systems.

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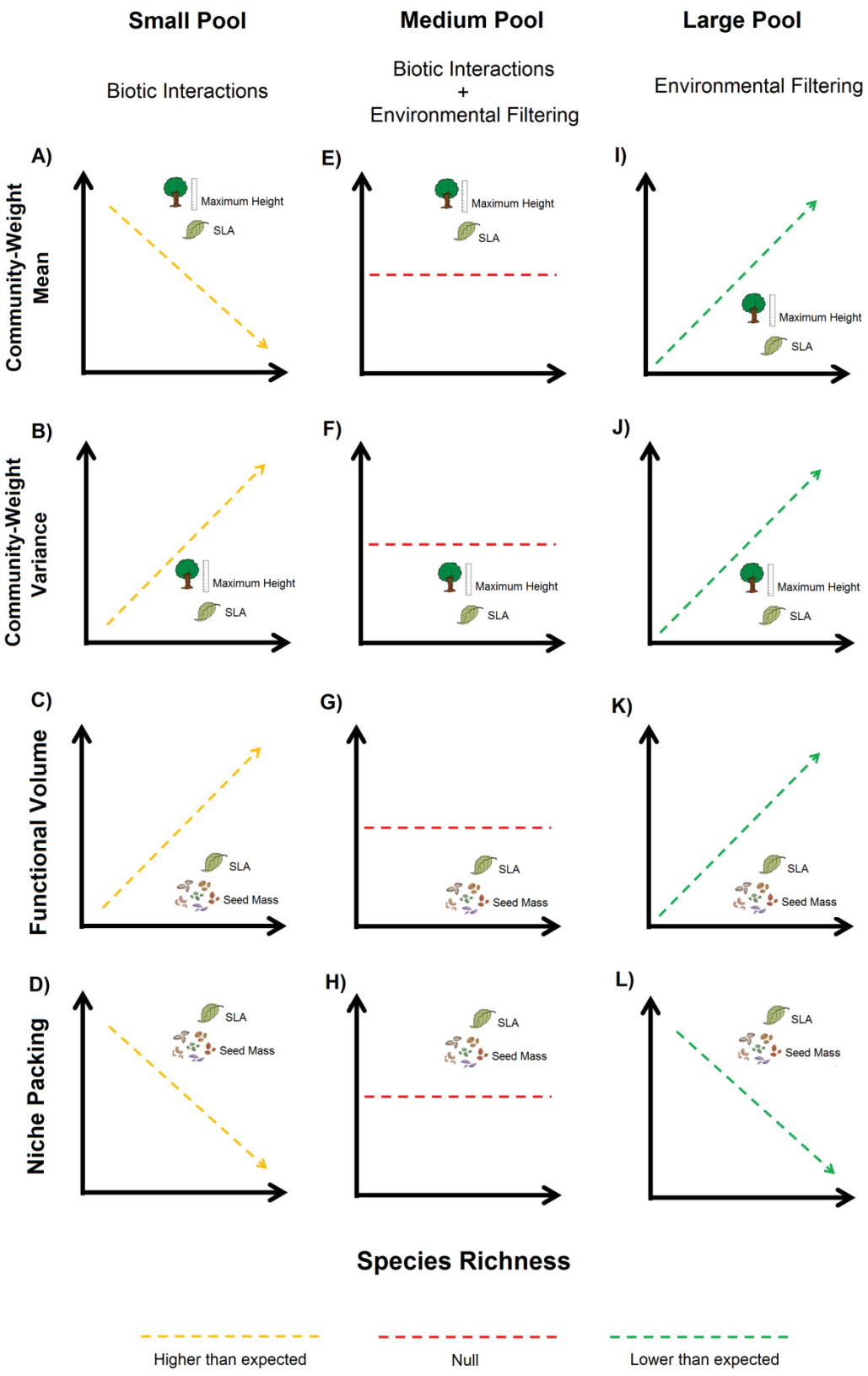


Figure 1 - Expected relationships between the species richness gradient, competitive exclusion (CWM e CWV), occupation (functional volume) and

packing of the functional space in relation to three different species pool sizes. In the small pool, biotic interactions are expected to prevail, then we hypothesize that: (A and B) the absence of higher competitors (higher plants and with high SLA) in plots of greater richness should be responsible for increase of species richness; (C) the functional volume should expand and be larger than expected at random as species richness increases, indicating that species occupy extreme portions of the functional volume to avoid niche overlap, thus ensuring coexistence; (D) the niche packing must be higher in plots richer (negative relation, indicating a better filling of the niche space) and larger than expected at random. In the medium pool, the transition between small and large pool must result in the capture of several processes acting at the same time, in order to generate random patterns. Thus, we do not expect to find relationships between different metrics and species richness (E – H). In the large pool, environmental filtering should predominate, then we expected a decrease in the effect of competitive exclusion on richness, so that the relationship between traits linked to competitive ability and richness will be positive (I- J); the functional volume should be less restrict as the species richness increase, to accommodate more species, but should be less than expected at random (K); the niche packing should be increase with species richness (equivalent to lower functional distance) and should be lower than expected at random (L).

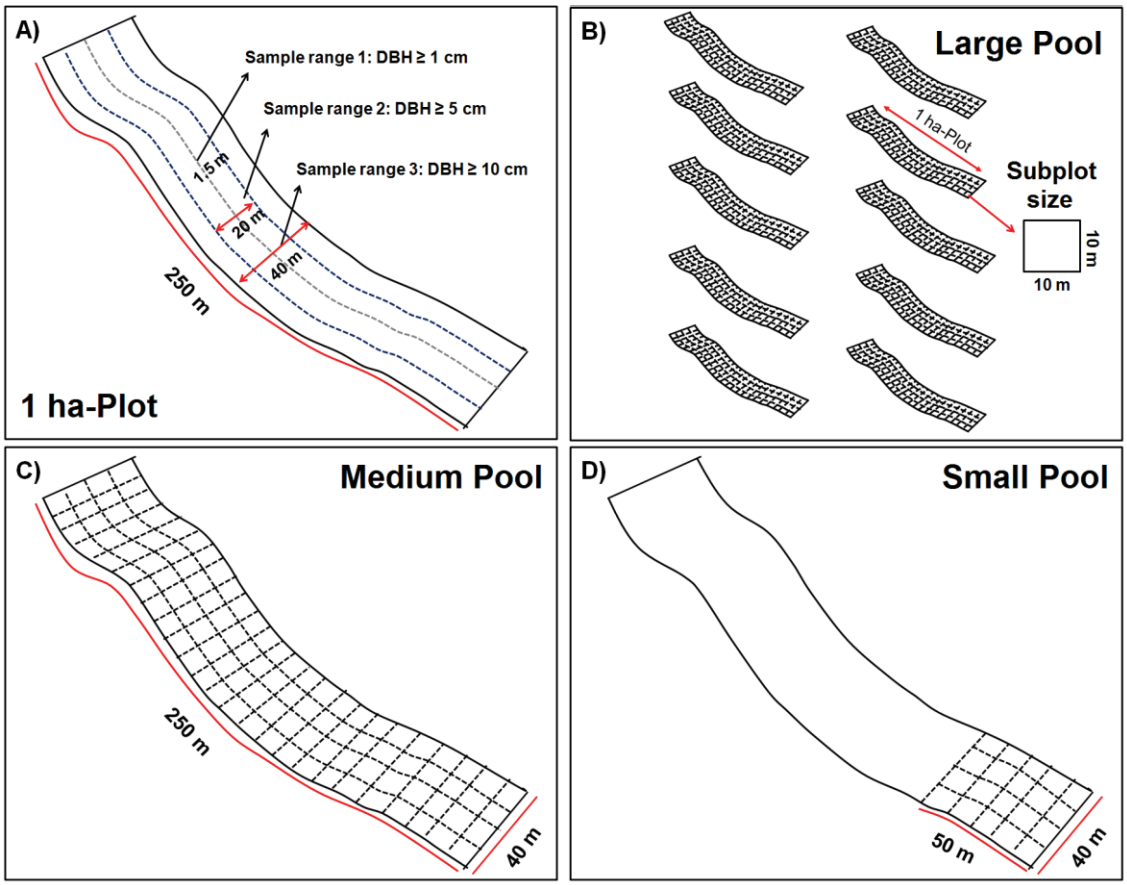


Figure 2 - Scheme representing: A) the delimitation of the sampling ranges in 1 ha-plots; B) the large species pool, defined as the total species in RAPELD module; C) the medium species pool, defined as the total species in each 1-ha plot and D) small species pool, defined as the total species in each 200 $m^2$ segments..

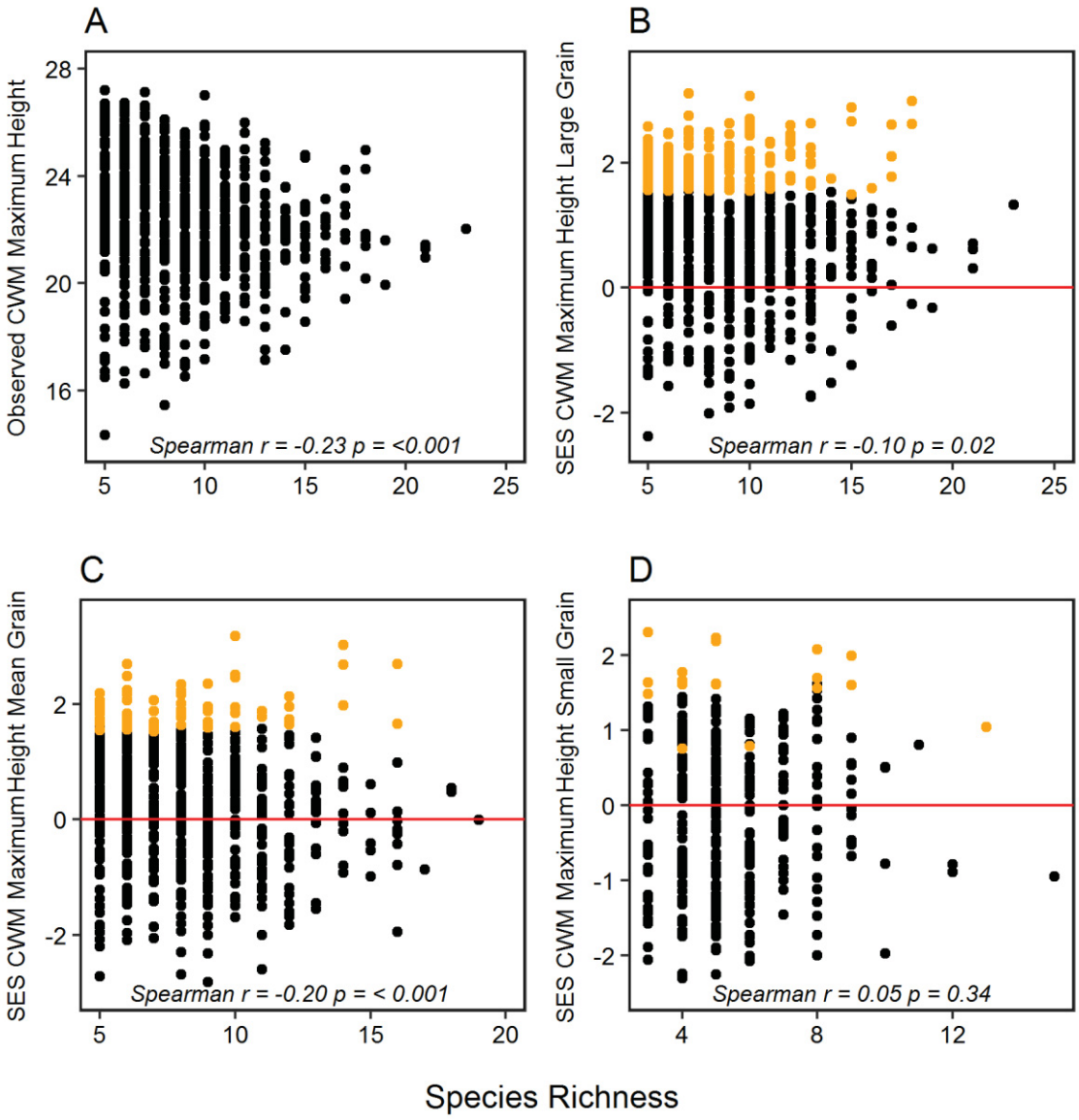


Figure 3 - The Spearman correlation between species richness and A) observed $CWM_{MH}$; B) *SES* $CWM_{MH}$ in large pool; C) *SES* $CWM_{MH}$ in medium pool; and D) *SES* $CWM_{MH}$ in small pool. The orange points represent subplots where $CWM_{MH}$ was significantly higher than expected (p > 0.95).

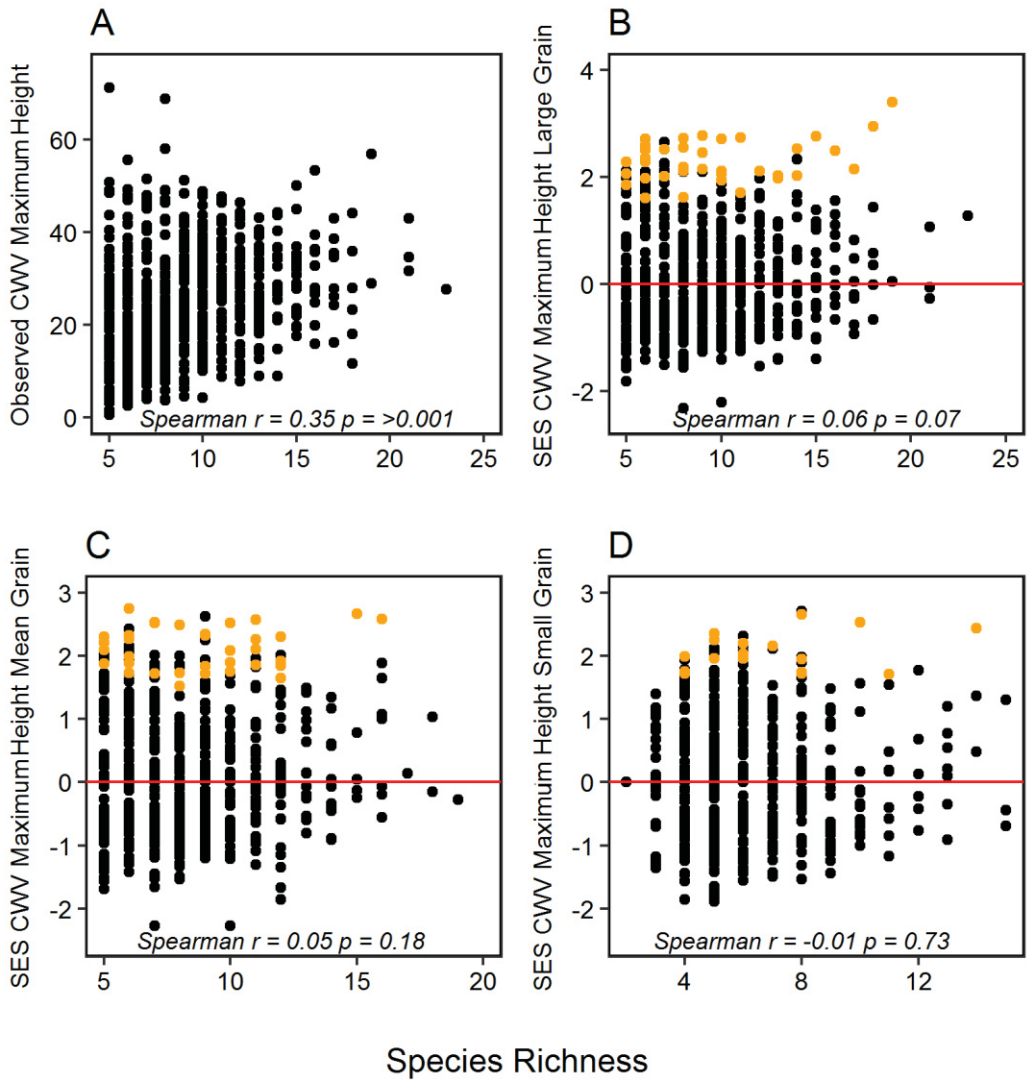


Figure 4 - The Spearman correlation between species richness and A) observed $CWV_{MH}$; B) *SES* $CWV_{MH}$ in large pool; C) *SES* $CWV_{MH}$ in medium pool; and D) *SES* $CWV_{MH}$ in small pool. The orange points represent subplots where $CWV_{MH}$ was significantly higher than expected (p > 0.95).

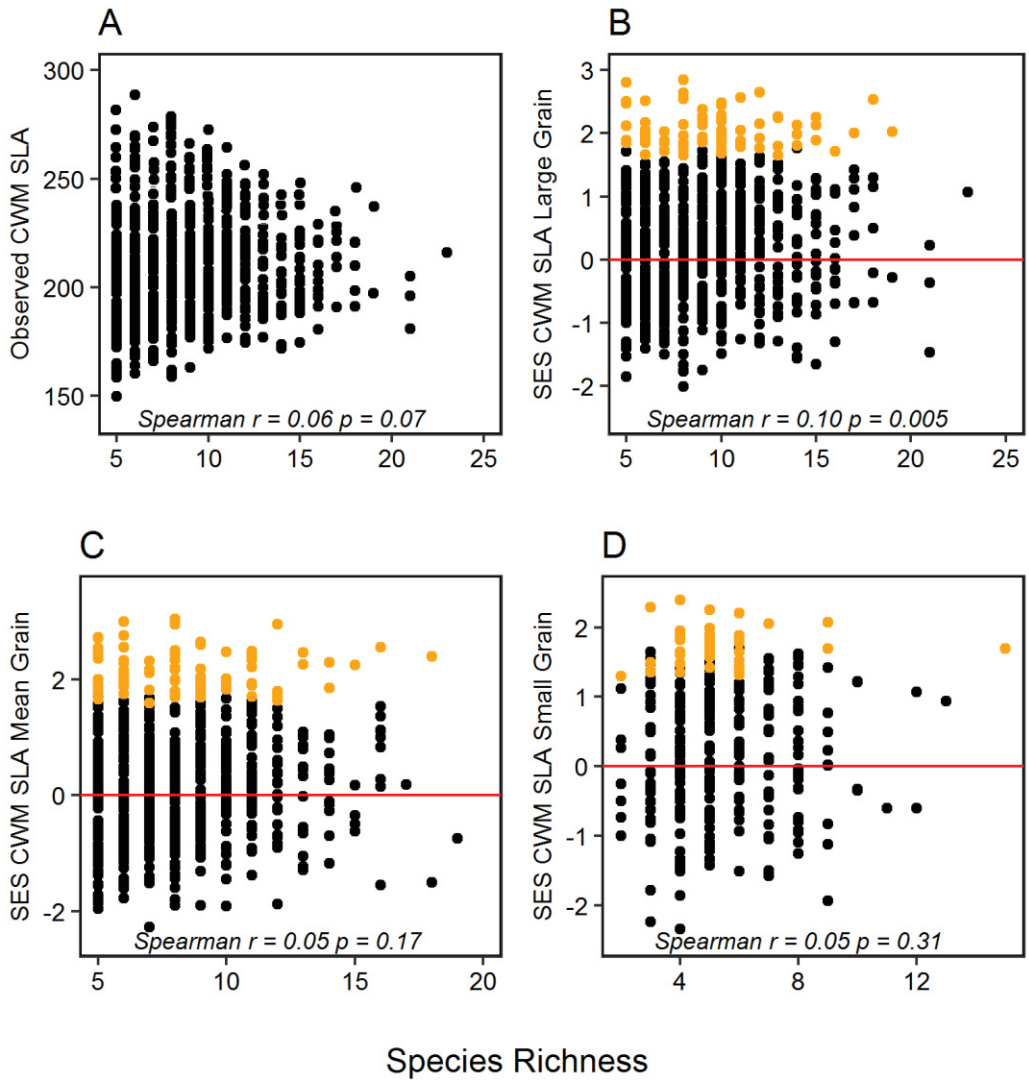


Figure 5 – Spearman correlation between species richness and A) observed $CWM_{SLA}$; B) *SES* $CWM_{SLA}$ in large pool; C) *SES* $CWM_{SLA}$ in medium pool; and D) *SES* $CWM_{SLA}$ in small pool. The orange points represent subplots where $CWM_{SLA}$ was significantly higher than expected ($p > 0.95$).

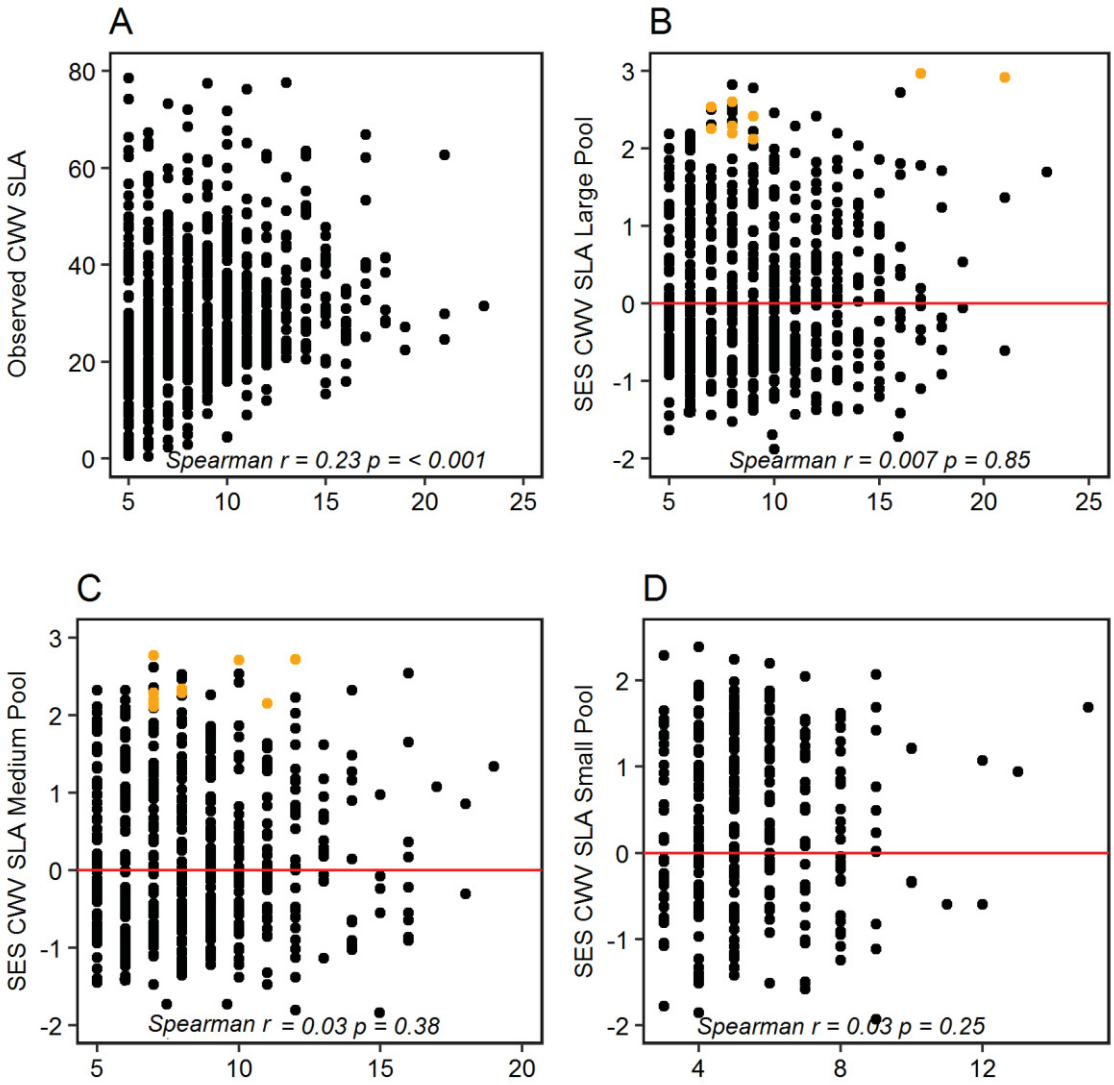


Figure 6 – The Spearman correlation between species richness and A) observed $CWV_{SLA}$ ; B) SES $CWV_{SLA}$ in large pool; C) SES $CWV_{SLA}$ in medium pool; and D) SES $CWV_{SLA}$ in small pool. The orange points represent subplots where $CWV_{SLA}$ was significantly higher than expected ($p > 0.95$).

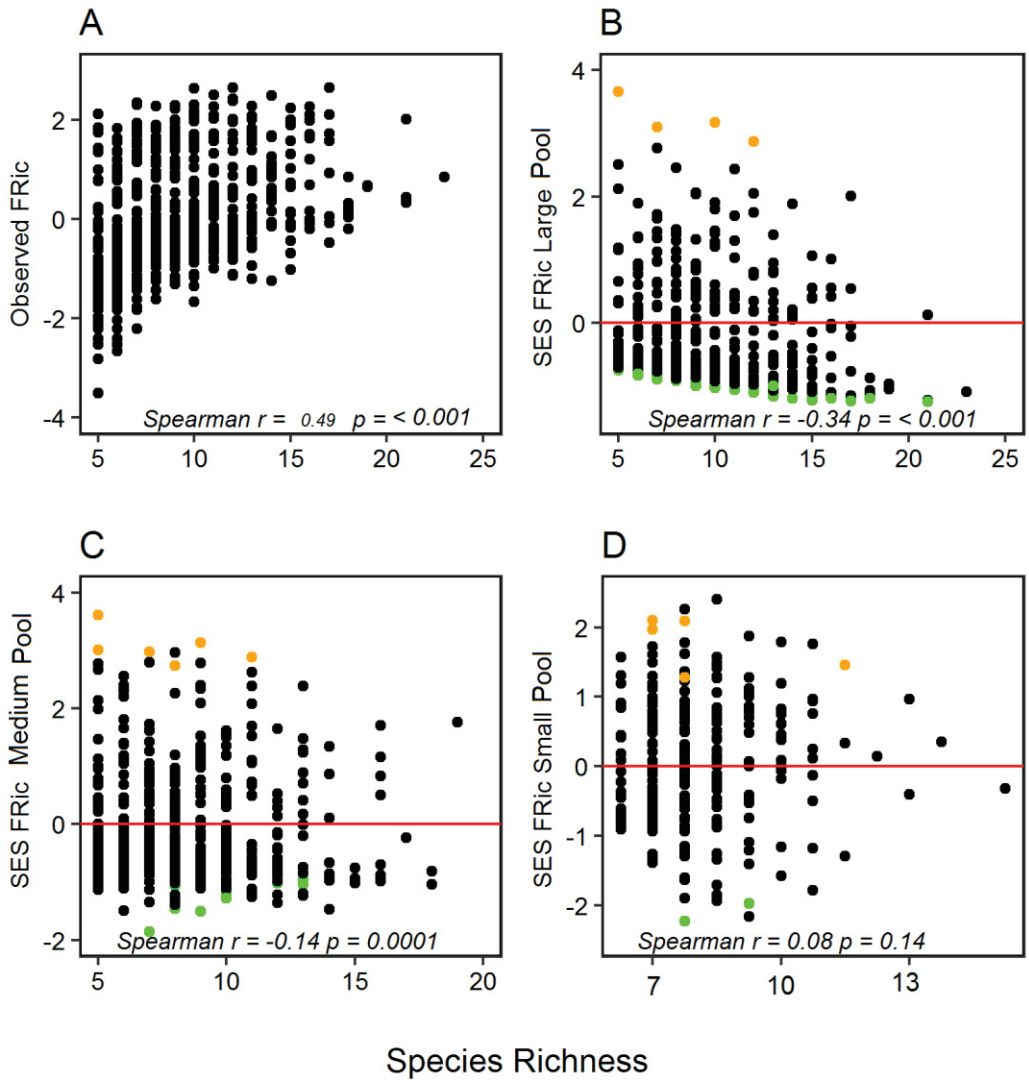


Figure 7- The Spearman correlation between species richness and A) observed *FRic* for seed mass and SLA*;* B) *SES FRic* in large pool; C) *SES FRic* in medium pool; and D) *SES FRic* in small pool. The orange points represent subplots where *FRic* was significantly higher than expected ($p$ > 0.075) and green points represent subplots where *FRic* was lower than expected ($p$ < 0.025).

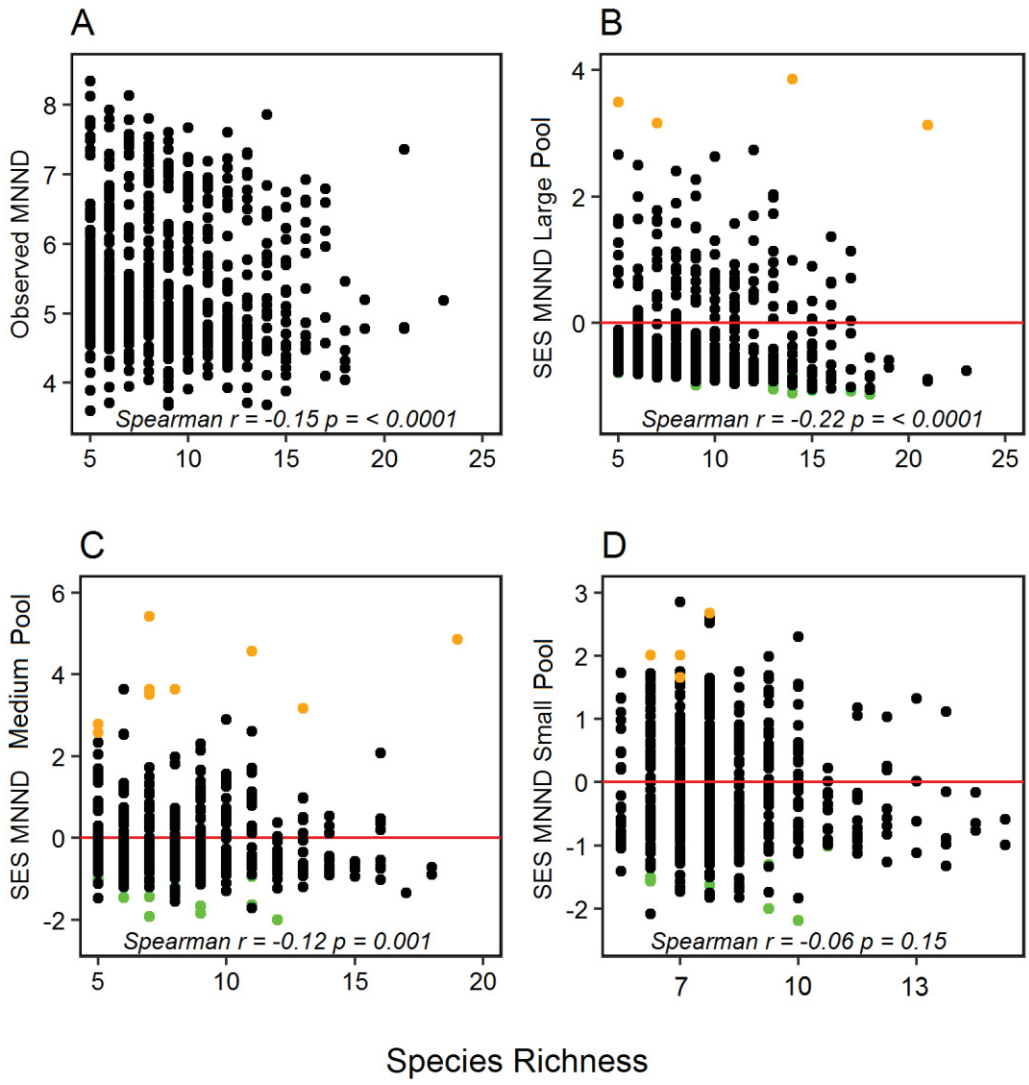


Figure 8 - The Spearman correlation between species richness and A) observed *MNND* for seed mass and SLA; B) *SES MNND* in large pool; C) *SES MNND* in medium pool; and D) *SES MNND* in small pool. The orange points represent subplots where *MNND* was significantly higher than expected ($p$ > 0.075) and green points represent subplots where *MNND* was lower than expected ($p$ < 0.025).

## 7. Appendix

Appendix A2- List of Atlantic Forest references used to collect seed mass data.

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# CAPÍTULO 3

## Setting the optimal size: The role of sampling effort in quantifying of functional structure of tree assemblages


### Abstract

Despite considerable interest in the application of plant functional traits to community assembly issues and ecosystem structure and function, there are still no protocols that define an adequate minimum sampling effort to measure key functional diversity metrics. Large samples require a lot of time and financial resources that are not always available; very small samples, in turn, can produce skewed results and limit the conclusions. Thus, knowing the effect of sample effort on key functional diversity metrics is a critical step in optimizing costs and ensuring accuracy in investigations. In this study, we tested the effect of sample effort, measured by variations in the number of sample units, in the composition and functional diversity of trees in relation to SLA, maximum height and seed mass to respond: 1) How do diversity and functional composition vary with the sample effort? 2) What is the minimum reliable sample for each trait that reflects the community's response to environmental gradients? We found that the functional composition was not affected, but the diversity increased with the reduction in the sample effort; the response of the functional composition to variations in environmental gradients was more affected than the functional diversity response, with the CWM of the maximum height being more affected and the CWM mass of the seed remained more accurate. We conclude that part of the results depends on how the metric is calculated and the goal. If the objective is the characterization of the functional composition it will probably be less affected by the sampling effort than the measures of functional diversity; if the objective is to analyze the response of species to environmental gradients a small number of sample units may bias the response.


Keywords: Rao. CWM. Maximum height. SLA. Seed mass.

## 1. Introduction

With the biodiversity crisis and the advancement of ecological theories that concern the assembly of communities, there has been a growing interest in the investigation of the role played by the species functional traits in the functioning and maintenance of the ecosystem processes, as well as in the species responses to climate change and environmental gradients (TILMAN *et al.*, 1997, DÍAZ & CABIDO, 2001; PETCHEY & GASTON, 2006; DÍAZ *et al.*, 2007; SUDING *et al.*, 2008, CORNWELL & ACKERLY, 2009). As functional traits provide a mechanistic view of communities, are relatively easy to measure and comparable between species and biological systems, functional diversity – defined as " the value and variation of species and their characteristics that influence the functioning of communities" (TILMAN, 2001) - has been preferred to other forms of diversity quantification (MCGILL *et al.*, 2006). In conjunction with functional composition, these two measures can be used to describe two complementary aspects of the community functional structure, such as the mean and dispersion of the functional traits within assemblies (RICOTTA & MORETTI, 2011).

Some protocols that standardize sampling methodologies for individual traits have been developed and suggested alternatives for selection of species and individuals within species (CORNELISSEN *et al.*, 2003; CHAVE *et al.*, 2009; PÉREZ-HARGUINDEGUY *et al.*, 2013). However, there are no protocols that define an ideal sampling effort for an accurate quantification of functional structure measures in different systems. Ideally, sample should include all individuals of all species and sample units, but the lack of financial resources and time are some of the factors that make this labor difficult (BARALOTO *et al.*, 2010, MESSIER *et al.*, 2010, CARMONA *et al.*, 2015). Since sample size is known to affect the number of *taxa* collected (MAGURRAN, 2013), it is expected that below-ideal sampling will underestimate functional composition and diversity measurements, and one consequence of this is the artificial increase of the relative importance of environmental filtering in the community structure (BARALOTO *et al.*, 2010). On the other hand, the lack of knowledge about the minimum sample, adequate to the purpose of the research, can

extend the work beyond what is necessary and thus generate expenses that could be applied in other purposes.

The trade-off between costs and effectivity of sample size in detecting assembly patterns have led many researchers to test the efficiency of different efforts and sampling methods in quantifying functional structure measures. Lavorel et al. (2007), proposed that, the greater the accuracy (and speed) in detecting dominant species in community, the better the quantification of diversity. Pakeman and Quested (2007) advocated the inclusion of species accounting 80% of the relative abundance in assemblies is sufficient for the measurement of quantitative traits with a minimum field effort. Baralotto et al (2010) compared different sampling methods and argued that, the effort in sampling at least one individual per species and sample unit may be essential for the characterization of mean and variance of plant species traits. In contrast, Carmona et al. (2015) suggested that a small sampling effort, since that it includes the intraspecific variability of traits, may be sufficiently accurate to characterize the assembly functional structure. A general conclusion reached in these studies is that the sampling should be proportional to the variability of the studied trait, that is, the more variable the trait, the more individuals and species should be sampled.

Another possible aspect of these studies is the focus on sample effort on the measures of the functional structure through the number of species within sample units or individuals within species, but not on the number of sample units. Sampling units may be sufficiently different from each other with respect to environmental factors to the point of influencing species turnover and, consequently, composition and functional diversity measures (LEPŠ *et al.*, 2011). It is expected that the amplitude of the environmental variation will decrease with the reduction in the number of sample units, thus making the capture of any response of the species to the environmental gradient dependent on the sample effort. It is sometimes difficult to establish a minimum number of sampling units for the survey; so many surveys are based on predetermined numbers (TOKESHI, 1993). However, knowledge of an ideal minimum number of sampling units prior to installation could save time and money. This is especially true when it comes to creating protocols for large research networks with several researchers involved (MAGNUSSON *et al.*, 2005).

In this study, we tested the effect of sampling effort, measured by variations in the number of sample units, in the functional composition and functional diversity of a species rich tropical forest to answer the following questions: 1) How do functional diversity and functional composition vary with sample effort? 2) What is the minimum reliable sampling that reflects the community response to environmental gradients?

## 2. Material and Method

### *2.1. Study area*

We carried out the study in the Guaricica Natural Reserve (25º19'15"S and 45º42'24"W), located in the municipality of Antonina, Paraná Sate, southern Brazil. The Reserve has 8,600 ha and is included in the Guaraqueçaba Environmental Protection Area, one of the largest protected and continuous remnant areas of the Brazilian Atlantic Forest (FERRETTI & BRITEZ, 2006). The climate is subtropical humid mesothermal; the mean temperature is 21°C in the warmer months and 18°C in the colder months, with annual rainfall around 2,000 to 3,000 mm and relative air humidity around 85% (MAACK, 2012). The vegetation in the region is dominated by Submontane and Lowland Dense Ombrophilous Forests (IBGE, 2012). Forests are marked by three well defined strata, canopies of 20-30 m in height, and tree species richness of more than 300 species (BORGO *et al.*, 2011).

### *2.2. Species data*

A RAPELD module has been established in a region of Submontane Dense Ombrophilous Forest in the reserve. This is a modification of the 0.1-ha plot method developed by Alwyn Gentry and adapted to long-term ecological research sites that allow rapid inventories (MAGNUSSON *et al.*, 2005). The RAPELD module consists of a set of ten 1-ha plots, systematically distributed in two rows with five plots, spaced 1 km from each other. Each plot had 250 m long by 40 m wide and its center followed the ground level curve, minimizing internal variations in topography and soil. Altitude between plots ranged from 20 to 470 m a.s.l., while slope inclination ranged from 6° to 22°.

Vegetation survey was done for two different plant sizes, using varying sampling ranges: Sampling range 2 - Ranges 20-m wide, concentric with the 1-ha plot, were used for sampling individuals with DBH ≥ 5 cm; Sampling range 3 – Ranges 40-m wide, representing the whole plot area, were used for sampling individuals with DBH ≥ 10 cm. The trees in the two ranges were measured, collected and identified at the species level.

For subsequent analyzes, we subdivided each 1 ha-plot into 40 x 50 m subplots, thus, each 1ha-plot generated five 200 $m^2$ subplots, totaling fifty subplots (5 subplots x 10 plots).

*2.3. Functional traits*

To characterize the functional diversity and composition of tree assemblages in each subplot, we chose three functional traits that describe the main axes of ecological strategies for plants (WESTOBY, 1998): specific leaf area (*SLA*), maximum height (*MH*) and seed mass (*SM*).

For *SLA* measurement, we collected five fully expanded leaves, exposed to sun and without herbivory, for five individuals of each species with DBH ≥ 5 cm (ranges 2 and 3), which summed 80% of the relative abundance in each 1 ha-plot. The newly collected leaves were scanned and the scanned images were used to measure the leaf area in the *ImageJ* software (RASBAND, 2012). After, they were oven dried for 72 hours and weighed. To obtain the *SLA* ($cm^2$) we divided the area by the dry weight of leaves and calculated the mean for each species. Thus, *SLA* for each species had a representation of at least five and at most fifty individuals (five individuals multiplied by ten 1 ha-plots).

Tree height (m) was obtained with electronic tape for all individuals of all species; when not possible the height was estimated by visual comparison. The maximum height (*MH*) observed in the study area for each species was used as trait.

The seed mass (mg) was obtained from several sources in the literature (Appendix A2 in chapter 2). We limited its collection to studies developed in the Atlantic Forest, in the dense ombrophylous forest subformation, and expanded to other subformations or formations only when the data were nonexistent in the first. When different values were found for the same species, we calculated the mean; in the absence of data for a species, we used the mean for the genus.

*2.4. Functional measures*

We calculate functional diversity and composition in the subplots for each trait separately using the *FD* package in *R software* (R CORE DEVELOPMENT TEAM, 2017).

As measure of functional diversity, we used an index based on Rao's quadratic entropy – Rao´s Q (BOTTA-DUKÁT, 2005) -, which incorporates the relative abundances of the species and their functional differences, calculated as:

$$\text{Rao} = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij}\, p_i\, p_j$$

where *dij* is the dissimilarity in trait values between each pair of coexisting species *i* and *j*, and *pi* and *pj* indicate the relative abundances of species *i* and *j*.

Rao'Q is a richness independent method, which is not directly affected by the number of traits in the analysis, i.e., it can be used with one or more traits. It is a modified version of the Simpson index, which considers the average functional distance between two randomly chosen individuals (BOTTA-DUKAT, 2005).

As measure of functional composition, we used the community-level weighted mean of trait values (CWM), calculated as:

$$\text{CWM} = \sum_{i=1}^{n} p_i \times \text{trait}_i$$

where $p_i$ is the relative contribution of species *i* to the community, and $\text{trait}_i$ is the trait value of species *i*.

This index is described as the mean of values present in the community weighted by the relative abundance of taxa bearing each value (RICOTTA & MORETTI, 2011), and reflects the traits mean values of the dominant species (DÍAZ *et al.*, 2007).

*2.5. Sampling simulations*

A resampling procedure was used to simulate a reduction in sample effort – i.e., in the number of the sample units - from the total of fifty subplots. Using the *sample* function in the *R software*, we selected, randomly and without replacement, sample units in multiple numbers of five to compose subgroups with eight different sample efforts: 45, 40, 35, 30, 25, 20, 15 and 10. This procedure was repeated one hundred times for each subgroup and each repetition we calculate Rao and CWM for the three traits on each sample unit composing the subgroups.

*2.6. Environmental variables*

To evaluate the influence of the environment on plants functional composition and diversity, we measured the slope- and soil-related environmental variables.

*Slope*: For slope measurement, we subdivided the 1-ha plots into sections of 10 m wide. Thus, each 1-ha plot was left with twenty five sections. The slope within the plots in the RAPELD module was obtained with electronic tape and clinometer at georeferenced points and spaced 10 meters from each other, i.e., in each plot section. Slope was measured at four different points in each plot section. The four points mean was used as slope measure for each section. The slope value for each subplot, in turn, was represented by the mean of the angles obtained for the five sections composing each subplot. The mean raw slope values in each subplot were used to represent this variable.

*Soil nutrients*: A simple soil sample was collected on each subplot, totaling five samples per plot. The samples were taken at depths of 0 to 5 cm, 5 to 10 cm, 10 to 20 cm and 20 to 30 cm. The samples were submitted to following chemical analyzes, according to standardized methodology (EMBRAPA, 2006) (Appendix A): pH (measured in $CaCl_2$), Phosphorus (P, mg/$dm^3$), Carbon (C, mg /$dm^3$), Calcium ($Ca^{2+}$, cmolc/$dm^3$), Magnesium ($Mg^{2+}$, cmol/$dm^3$), Sodium ($Na^+$, cmolc/$d^{m3}$), Potassium ($K^+$, cmol/$dm^3$), base sum (BS, cmolc /$dm^3$), base saturation (v,%), potential acidity ($H^+ + Al^{3+}$, cmolc/$dm^3$), Aluminum ($Al^{3+}$, cmolc /$dm^3$) and Aluminum saturation (m,%). As the use of soil nutrients by plants occur in the first layers deep, it was decided to use the soil average obtained in 0 to 20 cm deep. To reduce the dimensionality of soil nutrients variables, we

performed a principal component analysis (PCA) and used the axes, selected by the *Broken-stick* criterion, as explanatory variables (Appendix B1 in chapter 1).

*2.7. Statistical Analysis*

Above all, we tested the normality in the distribution of the variable responses by the Shapiro-Wilk test and the homoscedasticity of the variances by the Levene test. The response variables that did not show normal distribution were log - transformed. To the data whose assumption of normality and homogeneity of variances was not reached, we applied non-parametric analyzes.

In order to analyze how do functional composition (CWM) and diversity (Rao) vary with sample effort, we used the Kruskal-Wallis non-parametric test, followed by Dunn's post hoc test.

To find out what is the minimum reliable sampling that reflects the community response to environmental gradients, we used two-step linear models. In the first step, to find out which predictor variable influences the observed Rao and CWM, we used the most complete sampling effort (50 sample units) and selected the linear models that presented the lowest delta AIC using as response variables the Rao and CWM for each trait. As predictor variables, we used the PCA axes of soil nutrients plus slope. The predictor variables were standardized by subtracting their mean values and division by the standard deviation. In the second step, we used the predictor variable present in the best model selected to test the accuracy of the different sample efforts in detecting the Rao and CWM relationship with the environmental gradient. In cases where the null model was the best model selected, we chose to use the variable of greater weight present in the models with Delta AIC < 2. The explanatory variables selected for each response was used in linear models for each trait of the one hundred simulations and for each sample size, that is, we made a total of one hundred linear models for each trait and sample effort.

The accuracy of the different sample effort was measured by estimating the standard error and a 95 % confidence interval. The determination

coefficients means ($R^2$) of the validated models and the standard error were plotted against the different sample efforts. Sampling efforts that remained within the 95% confidence interval and whose standard error remained as close as possible to zero were considered to be accurate.

All analyzes were conducted in the platform R v.3.4.0 (R Core Development Team, 2017).

## 3. Results

The results of the Kruskal-Wallis analysis showed that the mean of the CWM for maximum height ($CWM_{MH}$, ($H_{(7)}$ = 5.81, $p$ = 0.56), specific leaf area ($CWM_{SLA}$, $H_{(7)}$ = 2.79, $p$ = 0.9) and seed mass ($CWM_{SM}$, $H_{(7)}$ = 3.49, $p$ = 0.84) was not affected by the sampling effort (Fig 1a-c). On the other hand, the mean of Rao for maximum height ($Rao_{MH}$, $H_{(7)}$ = 383.16, $p$ = < 0.0001) and SLA ($Rao_{SLA}$, $H_{(7)}$ = 154.21, $p$ = < 0.0001) was significantly higher as the sample effort was reduced (Fig 2a,b). The Rao for seed mass ($Rao_{SM}$, $H_{(7)}$ = 31.86, $p$ = 0.00) was slightly affected by the different sample efforts (Fig 2c), showing a tendency to increase as the sample effort increased.

Soil environmental variables were represented by three axes of principal component analysis (PCA, Appendix B): PCA1 (40%), was represented by C, $H^+$+$AL^{3+}$ and $Al^{3+}$; PCA2 (23%), represented by m, v and BS and PCA3 (14%), represented by $Na^+$, $K^+$ and P. The variable that best explained the $CWM_{SM}$ and $CWM_{SLA}$ was PCA2. $CWM_{MH}$ was better explained by PCA3 and slope, $Rao_{SM}$ was better explained by PCA1, whereas $Rao_{SLA}$ and $Rao_{MH}$, by PCA3 (Table 1).

In relation to communities response to environmental variables, most striking differences were observed for CWM. Except for CWM maximum height ($CWM_{MH}$), the standard $R^2$ error of CWM seed mass ($CWM_{SM}$) and CWM specific leaf area ($CWM_{SLA}$) remained within the 95 % confidence interval (Fig 3a-c). The $R^2$ of the $CWM_{MH}$ decreased with the reduction of the sample effort, although it remained significant, and was even more sensitive to the reduction of the sample effort, since the limit considered valid for the capture of the relationship between $CWM_{MH}$ and soil variables (PCA3 and slope) was 45

sample units (Fig 3a). The $R^2$ of the $CWM_{SLA}$ increased with decreased sample effort, and was the most affected of the three, and no sample effort could be considered ideal to maintain its accuracy (Fig 3b). In contrast, the $R^2$ of the $CWM_{SM}$ was the one that presented the lower variation; the standard error remained close to zero until the removal of fifteen sample units. This $R^2$ increased considerably in the lower sampling effort (10 sample units), but, instead, the standard error was also higher (Fig. 3c).

In general, we found that, for the three traits analyzed, the Rao determination coefficient ($R^2$) was not significantly altered by the variations in the sample effort. In addition, the standard error was kept within the 95% confidence interval for the three traits. The $R^2$ for $Rao_{MH}$ was more sensitive to variation in sample size; its accuracy was maintained until the removal of five sample units, that is, the minimum reliable number of sample units to capture the maximum height response to the environmental variation is 45 (Fig. 4a). Although not significant, the $R^2$ for $Rao_{SLA}$ was the second most affected: its accuracy was maintained until the removal of ten sample units (Fig. 4b). Among the three traits analyzed, $Rao_{SM}$ was the least affected and the use of twenty-five sample units still kept the standard error very close to zero, although the relationship was also not significant (Fig. 4c).

## 4. Discussion

The way in which sample effort influences diversity metrics can be determinant for the costs (financial and time) involved in performing realistic samplings. Considering this, in this study, we started an investigation to evaluate how different sampling efforts, measured by variations in the number of sample units, influence composition (CWM) and functional diversity (Rao) measures of three plants functional traits (maximum height, SLA and seed mass), as well as the response of the species to environmental gradients in this tropical forest.

In general, we observed that for the CWM, the median was the same among the different sample efforts; however, the determination coefficient ($R^2$) of CWM of each trait was relatively different among sample efforts; In contrast,

the means of Rao was quite different between two traits (SLA and MH), but the Rao $R^2$ of these variables was practically the same through the different sample efforts.

*b. How does composition and functional diversity vary with sample effort?*

The functional composition, measured through CWM, of the three traits did not change with variations in the sample size. This metric is obtained by multiplying the traits means of the species by their relative abundance in the community, a procedure that attributes greater weight to the dominant species and obfuscates the rare species; thus, the functional composition of the communities is described essentially by the dominant species traits. This metric is in accordance with the mass ratio hypothesis (GRIME, 1998), which states that the traits of dominant species are the most important determinants of ecosystem functioning, while those of subordinate species are very less important. Due to this, is a metric that has been very useful in assessing the dynamics of communities and ecosystem properties (DE BELLO *et al.*, 2005; GARNIER *et al.*, 2007; QUÉTIER *et al.*, 2007).

In terms of sampling, dominant species are generally well represented (MAGURRAN, 2013), regardless of the number of sample units, which could explain the invariability of the CWM through the different sampling efforts. Studies that assessed differences in sampling by varying species abundance also noted that CWM is generally less affected by the sampling method (LAVOREL *et al.*, 2007). This leads us to suggest that the functional composition of the communities can be well characterized even with a reduced number of observations, similar to findings of Carmona *et al.* (2015).

In relation to the functional diversity, the pattern observed was the reduction of $Rao_{MH}$ and $Rao_{SLA}$ with the increase of the sample effort, which is not surprising. In fact, although it is independent of richness, functional diversity can indirectly both increase and decrease with increasing species richness (BOTTA-DUKAT, 2005). This is possibly due to a property of functional diversity, measured through Rao's quadratic entropy: it is influenced by diversity based on species abundance and differences between species pairs. In this

way, the introduction of a new species in the community increases diversity based on abundance, while it may decrease the average dissimilarity between species, reducing functional diversity (BOTTA-DUKAT, 2005). Although we did not consider species richness here, the sample effort is known to affect the number of *taxa* collected (MAGURRAN, 2013), and the pattern of Rao decrease with increased sample effort may reflect the loss of dissimilarity between species, usually captured in smaller samples.

It is worth noting that the greater the variability of the trait, the greater should be the sampling effort (LAVOREL *et al.*, 2007; PAKEMAN & QUESTED, 2007; BALAROTTO *et al.*, 2010; CARMONA *et al.*, 2015). Vegetative traits such as height and especially leaf traits tend to be filtered within communities, that is, values are similar among dominant ones (GRIME, 2006). On the other hand, although we have not observed variation for seed mass in our data, regeneration traits are often variable among dominant ones (GRIME, 2006), and this leads to instability of functional diversity measures, depending on the method used to weight their characteristics in the calculation of indices (LAVOREL *et al.*, 2007).

c. *What is the minimum reliable sampling that reflects the community response to environmental gradients?*

The relationship between CWM of the three traits and the environmental variables seems to have been more affected by the reduction in sample effort than the CWM mean. As part of the variability in functional structure indicators along environmental gradients result of changes in species identity and abundance along the gradient (LEPŠ *et al.*, 2011; KICHENIN *et al.*, 2013), we believe that the variation found in relation to the determination coefficient ($R^2$) of the CWM, through the sampling efforts, can be explained by the dissimilarity in the composition of species that respond differently to environmental gradients. Simulations to resample random sample units may result in the selection of subplots with their own environmental characteristics that filter different subsets of species.

We also found that the $R^2$ of the $CWM_{SLA}$ and $CWM_{SM}$ increased considerably in relation to the decrease of the sample effort, even becoming

significant. In the study of Carmona et al (2015), the lower sampling effort (in this case, based on the number of individuals per plot) led to much better estimates of the functional structure in terms of precision and bias, and a more precise description of the changes in the functional structure through the environmental gradient than larger sampling intensities. In our study, however, the observed pattern does not necessarily indicate that the capture of community response to environmental gradients occurs at smaller samplings; besides increasing the error in relation to larger samples, at least for the $CWM_{SM}$, there is the mathematical bias behind the coefficient of determination, which tends to increase with decreasing sample *n* (GOTELLI & ELLISON, 2004). Perhaps others accuracy measures should be taken into account in order to confirm this conclusion.

Despite variations in mean values of Rao, we found that its $R^2$ was relatively constant in the face of changes in sample effort, that is, regardless of the number of sample units used to capture the relationship between functional diversity and environmental gradients, there was no tendency to increase or decrease the coefficient of determination. This pattern has also been observed for aquatic macroinvertebrate communities and can be attributed to functional redundancy within these communities (BADY *et al.*, 2005; SCHMERA *et al.*, 2009; PERU & DOLÉDEC, 2010).

## 5. Conclusions

In general, adequate sampling will depend on the question / objective of the research and the variability of traits in question. If the objective is simply to describe the functional composition, the sample size, according to our results, it does not seem to influence that purpose. This is probably due to how the functional composition metric (CWM) is calculated. For the functional diversity (Rao), depending on the traits, variations in the number of sample units may result in the decrease or increase of this index, so that it is essential to keep in mind the question to be asked and the knowledge of the variability between species of the trait considered, since the Rao indices takes into account the dissimilarities between species. As the higher trait variability, the greater the number of individuals that must be selected to adequately estimate the value of

the local species traits (CARMONA *et al.*, 2015) and, consequently, increasing the number of sample units better the characterization of this variation.

Once the objective is to analyze the community response to environmental gradients, larger sampling should be more accurate due to the smaller error observed in our data. In addition, smaller samplings may result in very short or non-existent environmental gradients, making it difficult to visualize this response, besides inflating the $R^2$ inducing biased results.

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Table 1 - Summary of the selected models for the most complete set of fifty sample units.

| **Response variable** | **Predictor Variable** | **$R^2$** | ***P* value** | **Predictive variable of greater weight** |
|---|---|---|---|---|
| CWM Maximum Height | PCA3 + Slope | 0.25 | 0.00 | PCA3 |
| CWM Specific leaf area | NULL | - | - | PCA2 |
| CWM Seed mass | PCA2 | 0.03 | 0.11 | PCA2 |
| Rao Maximum Height | PCA3 | 0.16 | 0.00 | PCA3 |
| Rao Specific leaf area | PCA3 | 0.10 | 0.07 | PCA3 |
| Rao Seed mass | PCA1 | 0.01 | 0.20 | PCA1 |

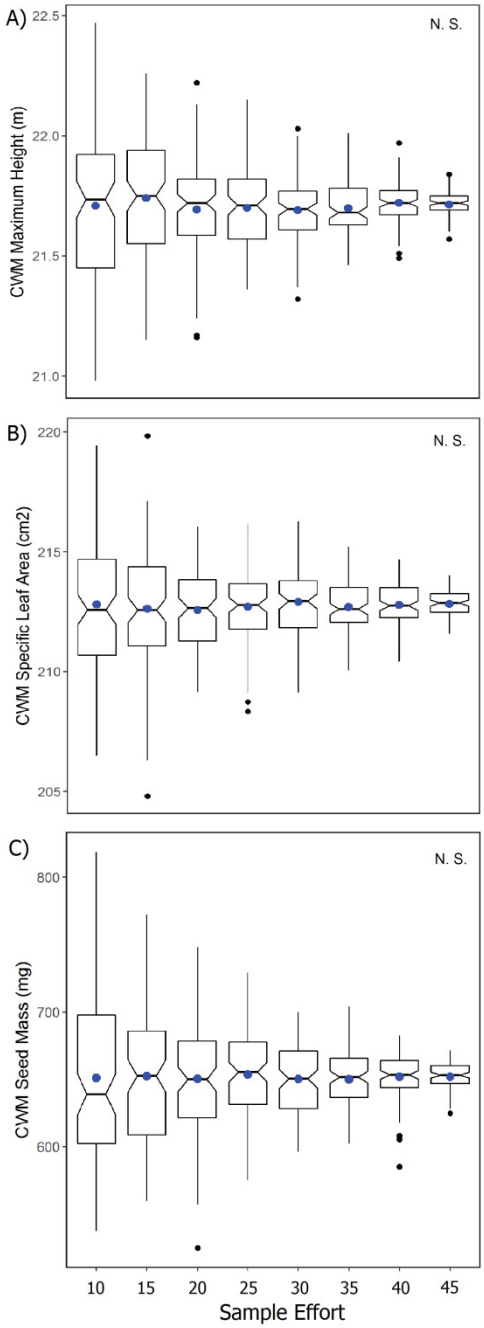


Figure 1 - Boxplots representing the variance of the functional composition (CWM), through eight different sampling efforts (number of sample units), for the following traits A) maximum height; B) specific leaf area; C) seed mass. The notches in the boxplots represent a 95% confidence interval calculated around the median; the blue points represent the CWM means for each sample effort; N.S. non-significant differences (*Kruskal-Wallis* test).

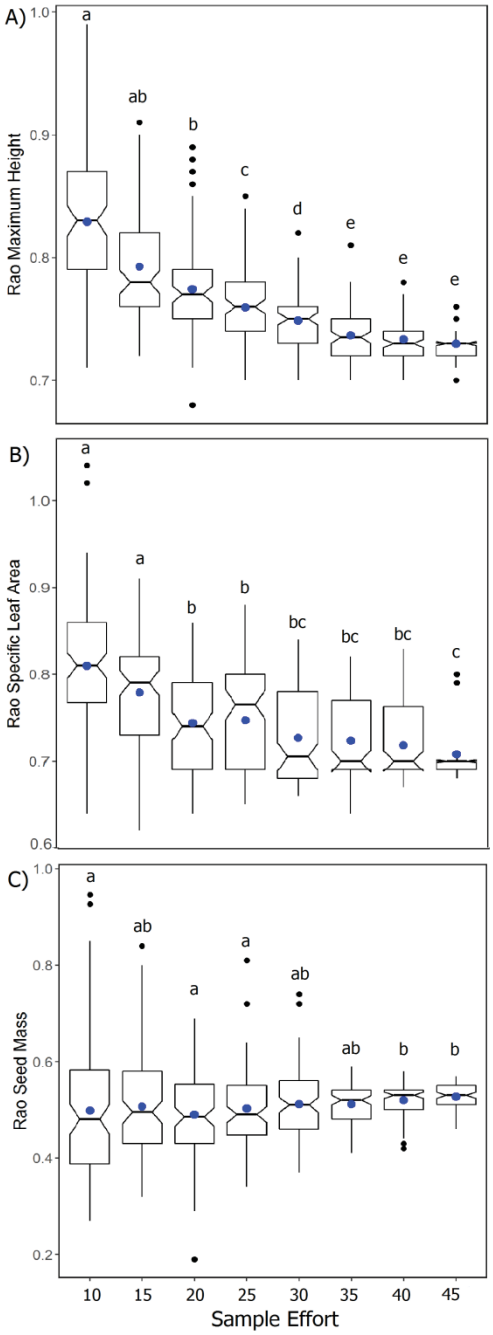


Figure 2 - Boxplots representing the variance of the functional diversity (Rao), through eight different sampling efforts (number of sample units), for the following traits: A) maximum height; B) specific leaf area; C) seed mass. The notches in the boxplots represent a 95% confidence interval calculated around the median; the blue points represent the Rao means for each sample effort. The letter code represent the groups that differ according to *Dunn's* post hoc test (followed the *Kruskal-Wallis* test).

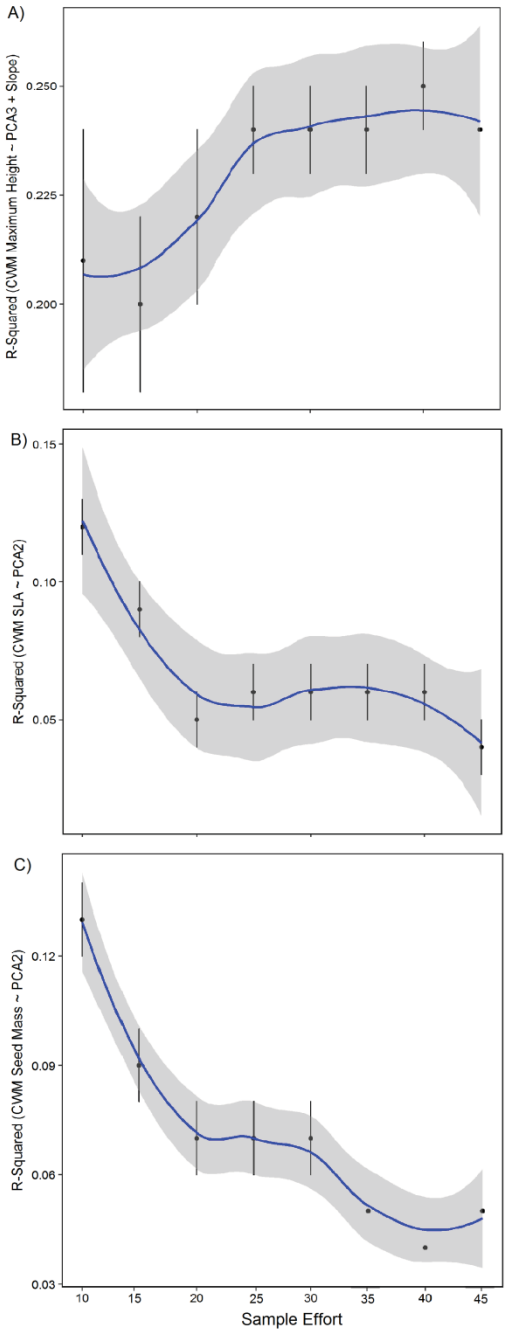


Figure 3 - Effect of reducing the sampling effort to capture the relationship between functional composition (CWM) and environmental variables of the following traits. A) maximum height; B) specific leaf area, C) seed mass. The black points represent the mean of $R^2$ for one hundred linear models of each simulation; the bars around the mean represent the standard error; smooth lines represent a 95% confidence interval.

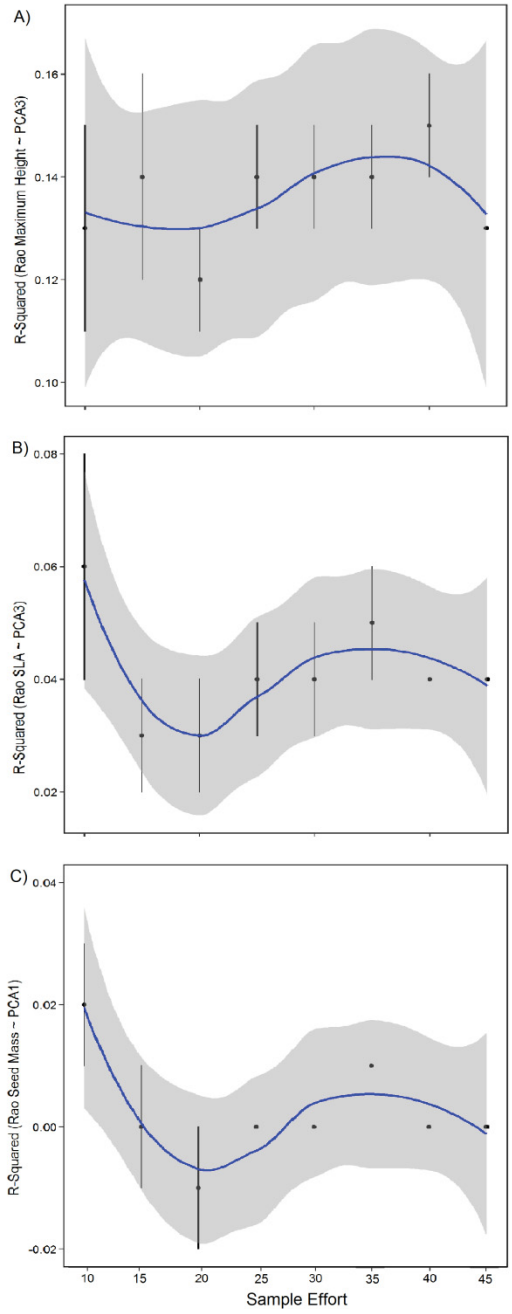


Figure 4 - Effect of reducing the sampling effort to capture the relationship between functional diversity (Rao) and environmental variables of the following traits: A) maximum height; B) specific leaf area, C) seed mass. The black points represent the mean of $R^2$ for one hundred linear models of each simulation; the bars around the mean represent the standard error; smooth lines represent a 95% confidence interval.

## Conclusões Gerais

Esta tese foi motivada pelo interesse de conhecer os processos que geram e mantêm a alta diversidade de espécies de plantas da Mata Atlântica. Nós utilizamos duas abordagens para analisar o papel dos processos de nicho na composição e riqueza de espécies, as quais forneceram resultados diferentes e ressaltam a variedade de fatores que podem influenciar na captura desses processos; por um lado, podemos dizer que a variação na composição (diversidade beta) parece ser afetada por interações bióticas, como a competição, e pela partição de recursos, processos que foram dependentes da escala espacial e da ontogenia; por outro lado, a riqueza de espécies foi principalmente associada à filtragem ambiental. É indiscutível que a atuação de um processo não impede outro, e os nossos resultados não só fornecem evidências da multiplicidade de processos influenciando os padrões de diversidade, como também ressaltam que a escolha da abordagem pode determinar o resultado. Aliado a isso, podemos ainda destacar o papel das diferentes escalas espaciais e pools de espécies. Nós demonstramos que redução da escala espacial evidencia as interações entre espécies, como observado para a composição, enquanto que o aumento da escala espacial captura a filtragem ambiental, o que foi observado para a riqueza de espécies. Entretanto, o aumento da escala espacial também pode capturar os efeitos das interações bióticas na composição de espécies. Somado a essa amplitude de fatores, nós demonstramos no terceiro capítulo, que diferenças no esforço de amostragem, entre outras coisas, podem influenciar em algum grau a captura da resposta das espécies aos gradientes ambientais, de maneira que a definição de um esforço amostral adequado deve ser outro fator com possíveis implicações na análise processos de nicho.

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